PERCEPTUAL AND ATTENTIONAL CONSTRAINTS ON 1:1 BIMANUAL COORDINATION

A Dissertation

by

ATTILA J. KOVACS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2010

Major Subject: Kinesiology

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Chair of Committee,	Charles H. Shea
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ABSTRACT

Perceptual and Attentional Constraints on 1:1 Bimanual Coordination. (May 2010)

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Two experiments were conducted in an attempt to further the understanding of how previously identified intrinsic constraints and perceptual factors interact in influencing the learning and performance of various bimanual coordination patterns.

The purpose of Experiment 1 was to determine the influence of Lissajous feedback on 1:1 bimanual coordination patterns (0^o, 90^o, 180^o phase lags) when the movement amplitudes of the two limbs were different. Participants coordinated rhythmic movements of their forearms while being provided separate feedback for each limb (no-Lissajous group) or integrated feedback (Lissajous group). Data from Experiment 1 supports the notion that the lead-lag relationship as well as amplitude assimilation between limbs observed in the literature can be partially attributed to the visual-perceptual factors present in the testing environment. When participants are provided integrated feedback in the form of Lissajous plots and templates much of the lead-lag and amplitude assimilation effects were eliminated and relative phase error and variability were also greatly reduced after only 3 min of practice under each condition.

Results from recent experiments suggest that when the salient visual information (Lissajous feedback) is removed, performance in bimanual coordination tasks rapidly deteriorates. The purpose of Experiment 2 was to determine if reducing the frequency of feedback presentation will decrease the reliance on the feedback and will facilitate the development of an internal representation that will improve performance when visual feedback is removed. Participants receiving reduced frequency feedback presentation were able to perform a delayed retention test with the feedback removed as well as the test with feedback present. Data from Experiment 2 demonstrates that salient extrinsic Lissajous feedback can effectively be combined with reduced frequency feedback presentation in a way that performance levels, when tested without the availability of feedback, match those obtained when tested in the presence of Lissajous feedback.

Taken together the present experiments add to the growing literature that supports the notion that salient perceptual information can override some aspects of the system's intrinsic dynamics typically linked to motor output control. The strong tendencies toward the intrinsic dynamics found in numerous previous bimanual movement studies and the difficulties in producing various coordination patterns may actually represent detrimental effects attributable to the perceptual information available in the environment and the attentional focus participants adopt. Given external integrated salient visual information participants can essentially tune-in and learn difficult bimanual coordination patterns with relatively little practice.

DEDICATION

To my wife Cristina, for her unconditional love and support throughout this journey.

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CHAPTER I

INTRODUCTION

Dynamical pattern approach to biological motions dwells on two key concepts: the intrinsic dynamics of the system and the behavioral or environmental information. Intrinsic dynamics refer to those behavioral patterns that emerge spontaneously from the cooperation among the systems' components as a result of nonspecific changes in an external control parameter (e.g. movement frequency). Behavioral information represents the influence of specific environmental parameters on the collective variable or order parameter dynamics. The extent to which intrinsic dynamics and environmental information cooperates or competes will determine the behavior pattern actually produced by the system. A dissipative dynamical system is one whose phase space decreases in time, phase space being all the possible states of the system and their evolution in time. For a given task and a given range of the control parameter, certain states of the system are more stable (preferred) than others. These states are named attractors and each attractor has a region in phase space to which all initial conditions will converge.

Within the coordination dynamics framework, a theoretical model that captures how biological systems evolve from one state to another (phase transition) has been forwarded by Haken, Kelso and Bunz (1985). The behavioral task used was the oscillation of both index fingers at various pacing frequencies determined by an external

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This dissertation follows the style of the *Journal of Experimental Psychology: Human Perception and Performance.*

control parameter. When the fingers are moving simultaneously towards or away from each other, and the movement is performed using homologous muscle groups, it is defined as in-phase ($\Phi = 0^o$). Movement in the opposite direction is defined as anti-phase ($\Phi = 180^o$). As the pacing frequency was increased so did the variability (standard deviation) of the relative phase between the fingers, when performing the anti-phase coordination pattern. For a given critical frequency a sudden qualitative change in movement pattern was observed from anti-phase to in-phase. The change occurs because the phase space of the attractor dissipates and the critical fluctuation pushes the system into the phase space of another attractor that is more stable at the given values of the control parameter (frequency). The resulting pattern is named a collective or cooperative effect which arises without any external instruction from the control parameter. According to this theoretical model (HKB model), the intrinsic coordination dynamics of bimanual movements are such that certain coordination patterns (in-phase and anti-phase) are easier to perform than others (e.g., 90^o relative phase) with the focal point being on the stability (low standard deviation) of the relative phase between the oscillating components. While the in-phase and anti-phase patterns have been shown to be relatively stable states, in-phase being more stable than anti-phase, a relationship of 90^o relative phase has been shown to be extremely unstable and consequently hard to perform and requiring extensive practice to learn (Swinnen, Lee et al., 1997, Zanone & Kelso, 1992; 1997).

Difficulties in performing coordination patterns other than in-phase and anti-phase have been traditionally attributed to the attraction toward the intrinsic dynamics (in-

phase and anti-phase), various structural constraints such as neural crosstalk (Kennerley et al., 2002) and/or time delays associated with the integration of the afferent and efferent signals due to anatomical connectivity (Banerjee & Jirsa, 2006). More importantly these limitations were thought to arise from the action components of the perception-action system. More recently, however, Kovacs and colleagues (Kovacs, Buchanan, & Shea, 2009a-c, in press) have demonstrated that some of the difficulties in performing a wide variety of bimanual coordination patterns should be viewed in terms of the perceptual information available and the attentional demands imposed by the testing environment.

Experimental hypotheses

Two experiments are proposed, which were designed in an attempt to further the understanding of how previously identified intrinsic constraints and perceptual factors interact in influencing the performance of various bimanual coordination patterns.

Experiment 1 was designed to determine if the strong coupling asymmetries manifested between dominant/non-dominant limbs and between limbs moving with disparate amplitudes can be overcome with (a) the provision of salient integrated perceptual feedback (Lissajous plots and a cursor representing the current relative phase between the two limbs) and (b) the attentional demands (vision of limbs, metronome) are reduced. Previous research (Peper, de Boer, de Poel, & Beek, 2008) has shown that for bimanual coordination tasks amplitude manipulations whereby the limbs move at unequal amplitudes the strength of the asymmetric coupling increases with movement amplitude. That is, the limb moving at the smaller amplitude is more strongly affected

by the contralateral limb than vice versa. Additionally, there is evidence that not only differences in amplitude, but directing attention to one or the other limb also modulates the asymmetric coupling between the limbs (de Poel, Peper, & Beek, 2008). It is hypothesized that asymmetric coupling between the limbs arises in part from perceptual-attentional demands present in the testing environment.

The purpose of Experiment 2 was to determine the degree of reliance on the salient and integrated visual feedback used in recent experiments. Results from Kovacs et al. (2009a) suggest that when the salient visual information (Lissajous feedback) is removed, performance rapidly deteriorates. It was hypothesized that the presentation of this type of augmented visual feedback might result in increased reliance on the feedback during practice, to the detriment of developing an internal representation of the required coordination pattern. Therefore, the purpose was to determine if reducing the frequency of feedback presentation will facilitate the internalization of such representations. Consistent with the predictions of the guidance hypothesis (Salmoni, Schmidt, & Walter, 1984) it was hypothesized that presenting 50% reduced frequency feedback in a fading schedule will improve performance on a subsequent test when visual feedback will be removed (Winstein & Schmidt, 1990).

CHAPTER II

LITERATURE REVIEW

Major questions in motor control

One of the most distinctive features of living organisms is the high degree of coordination among the constituting parts. Another fundamental characteristic is the ability to adjust behavioral patterns continuously to environmental requirements. At any level of description (i.e. molecular, cellular, muscular, systemic, biomechanical, behavioral etc.) many interacting components can be identified. Thus, the system has a multitude of degrees of freedom that are constantly interacting within and across levels. The complexity of this system can be addressed at many different levels, however, the identification of all the components across all levels of analysis might be too difficult. Even if knowing the identity of all the interacting components the reconstruction of the dynamics of their interaction would be a very difficult thing to do even if it addresses a simple task. In complex biological systems it is generally not possible to determine the detailed behavior of every degree of freedom. The problem is to try and identify only the relevant parameters of the system, thereby reducing the unnecessary information (Schöner & Kelso, 1988). Nevertheless, the manner by which complex biological systems are coordinated to produce functionally specific ordered behavior or spatiotemporal patterns remains one of the great unsolved problems of biology.

Key concepts of Dynamic Patterns theory and the HKB model

Within the motor neuroscience literature, coordination dynamics theory attempts to describe at the lowest possible dimension the largest number of empirically observed

features of temporal patterns and to provide a minimal set of dynamical laws for pattern generation in complex biological systems (Schöner & Kelso, 1988). The base of this approach is the concept that biological systems are self-organizing, non-linear dynamical systems described from a synergetic aspect. Dynamical Pattern theory dwells on two key concepts, the intrinsic dynamics and behavioral (environmental) information. Intrinsic dynamics refers to those behavioral patterns which emerge spontaneously from the cooperation among the system's components as a result of nonspecific changes in an external control parameter (Haken et al., 1985). Behavioral information represents the influence of specific environmental parameters on the collective variable or order parameter dynamics. The extent to which environmental information and intrinsic dynamics cooperates or competes will determine the behavioral pattern actually produced.

Rhythmical behaviors are ubiquitous in biological systems and they are considered a good model of time-dependent behavior in nature (Kelso, 1995). Bimanual rhythmic coordination tasks have been used extensively in the research of human motor control. The study of bimanual coordination can be viewed as a window that allows us to gain insight into the highly complex and redundant organization of the nervous system.

A reference point in the development of the Dynamical Pattern approach was the seminal work of Haken et al., (1985), who developed a theoretical model of phase transitions in human bimanual movements (HKB model). The experimental system used was the bimanual finger coordination (Kelso, 1984), where the index fingers of both hands had to oscillate at a given frequency. Using this task as a reference, a few basic

concepts related to Dynamical Pattern approach can be defined. The oscillating frequency for the fingers is given by a metronome. When the fingers are moving simultaneously towards or away from each other, and the movement is performed using homologous muscle groups, it is defined as in-phase ($\Phi = 0^{o}$). Movement in the opposite direction is defined as anti-phase ($\Phi = 180^{o}$). As the pacing frequency is increased so does the instability (standard deviation of relative phase) of the anti-phase pattern and a sudden qualitative change in pattern or phase transition, from anti-phase to in-phase, is sometimes observed at a certain critical frequency. This phase transition occurs because the system is no longer able to perform the anti-phase pattern at the critical frequency and it switches to another pattern that is more stable at that frequency (Kelso, Scholz, & Schöner, 1986). The phase transition is called a collective or cooperative effect which arises without any external instruction. In this case the pacing frequency, referred to as control parameter, is an external variable that can induce changes in the system. However, the control parameter does not specify or contain the code for the emerging pattern, it simply pushes the system or promotes instabilities leading to a variety of possible states. Phase transition allows identifying the demarcation of various patterns while loss of stability is considered as evidence for self-organization. Thus, instabilities enables us to identify the dimension on which pattern changes occur, the so-called variable or order parameter (relative phase). Although the HKB model was originally developed to account for the transition observed in the coordination between two index fingers, the potential turned out to be generalizable to the coordination between different effector systems (e.g., arm and leg, Jeka & Kelso, 1995), single limb movement (Kelso,

Buchanan, & Wallace, 1991) and an external periodic stimulus (Byblow, Chua, & Goodman, 1995) and even the rhythmical swinging of limbs between persons (Schmidt, Carello, & Turvey, 1990). The fact that the transition from anti-phase to in-phase coordination was observed in these rather different cases indicates that the identified coordination principles are more general than the system in which they are embodied.

Researches employing a large number of experimental tasks have revealed remarkable temporal constraints (Kelso, 1984; Kelso & deGuzman, 1988) that limit spontaneous bimanual coordination to two relatively stable patterns. Coordination patterns of in-phase (relative phase between oscillating components, $\Phi = 0^{o}$) and anti-phase ($\Phi = 180^{o}$) have repeatedly been found to be inherently more stable and easy to perform without extended practice. Other coordination patterns (e.g. $\Phi = 30^{o}$ to 150^{o}) are quite difficult to perform and require more practice in order to achieve relatively stable performance (Zanone & Kelso, 1992; Yamanishi, Kawato, & Suzuki, 1980). This pattern of results has been modeled as nonlinearly coupled limit cycle oscillators (Haken et al., 1985) perturbed by stochastic forces (Schöner, Haken, & Kelso, 1986). The two stable states of the system (in-phase and anti-phase) have been labeled the intrinsic dynamics. Although such theoretical modeling initially did not link the functional aspect of the coupling between oscillators to any neuromuscular and/or cognitive process, researchers have been trying to reveal processes that may explain such functional coupling. Many studies have attempted to identify the nature of the constraints that limit the system to a bi-stable state as captured by the HKB model (Haken et al., 1985). Various constraints related to neuromuscular, perceptual and/or attentional factors have been identified.

Cognitive constraints on bimanual coordination

Some researchers view the basis for the functional asymmetry as mediated by attentional factors (Peters, 1989, 1994; Kinsbourne, 1970). Indeed, the role of attention in bimanual movements has been subjected to a good deal of experimental investigation (e.g., Hiraga, Summers, & Temprado, 2004; Summers, Maeder, Hiraga, & Alexander, 2008). Recent theorizing has attempted to link neural areas such as the anterior cingulate cortex to cognitive constraints that may impact the "functional representations" of muscles underlying sensorimotor coordination in general (Carson & Kelso, 2004). For example, when trained musicians (pianists) performed a familiar piece, increased activation was found in the SMA whereas when they performed unfamiliar pieces increased activation was found in the pre-SMA (Sergent, 1993) suggesting an increase in attention related processes. Further, Temprado, Zanone, Monno, and Laurent (1999) have demonstrated that the stability of the intrinsic dynamics (i.e. in-phase and anti-phase) as well as the difference between them depends on the attentional priority given to the coordination task. When attention to the bimanual task was somehow released (i.e. shared attention in a dual-task condition or focus on the secondary task) both intrinsic patterns showed a consistent increase in variability with higher increase for the anti-phase compared with the in-phase pattern. Conversely, when attention was directed to the bimanual task, variability of both patterns decreased with a stronger effect for the anti-phase pattern. Furthermore, these effects observed at the level of the coordination pattern were also reflected at the component level (individual limbs). However, there are also views arguing that while attentional factors undoubtedly play a role, they are not the

basis for the functional asymmetry (Carson, 1989; Allen, 1983; Amazeen, Amazeen, Treffner, & Turvey, 1997), but rather attention and handedness are related through their mutual effects on the bimanual coordination dynamics (de Poel et al., 2008)

Neuromuscular constraints on bimanual coordination

Another contribution to the coupling and stability characteristics of bimanual coordination has been argued to reside in forward commands and the interactions that arise from those commands as the result of shared neural pathways (Ridderikhoff, Peper, & Beek, 2005). The concept of neural crosstalk has been used to explain the findings of stability differences and phase transitions in various bimanual coordination patterns based on interactions in forward command streams in the highly interconnected and redundant organization of the nervous system (for review, see Swinnen, 2002). Neural crosstalk occurs during bimanual coordination when both hemispheres simultaneously send signals to the contralateral and the ipsilateral side of the body via the crossed and uncrossed cortico-spinal pathways. Depending on the type of coordination pattern performed the simultaneously descending signals to one limb via these pathways might be congruent, activating homologous muscles, or incongruent, activating non-homologous muscles (Cattaert, Semjen, & Summers, 1999; Kagerer, Summers, & Semjen, 2003). Additionally, crosstalk has been shown to occur between hemispheres (Kennerley et al., 2002). Activation levels of brain areas differ depending on the types of coordination patterns performed, with higher activation levels in some motor and pre-motor areas when an anti-phase coordination pattern was performed compared to when an in-phase pattern was performed (Jancke et al., 2000; Stephan et al., 1999).

Furthermore, de Oliviera, Gribova, Bergman and Vaadia (2001) have shown that during in-phase coordination the correlations between interhemispheric motor cortical areas (the motor areas activated simultaneously in both hemispheres) are much stronger than during anti-phase coordination. As Swinnen (2002) noted, this correlated activity between hemispheres could provide the neural basis of crosstalk between limbs, as observed at the behavioral level. Moreover, some research has shown that somatosensory feedback is not necessary to establish and maintain stable symmetric and asymmetric bimanual circle tracing patterns (Spencer, Ivry, Cattaert, & Semjen, 2005). Thus, one contribution to the coupling and stability characteristics of bimanual coordination clearly resides in forward commands and the interactions that arise from those commands as the result of shared neural pathways (Ridderikhoff, et al., 2005).

Coalition of constraints influencing bimanual coordination

Recent studies have favored the hypothesis that a coalition of constraints, ranging from high-level cognitive-perceptual to lower-level neuromuscular and directional, modulates stability of coordinated behavior. A debate still persists with respect to the nature (cooperative, competitive, or both) of these constraints. For example, neuromuscular constrains seem to modulate coordination stability differentially as a function of whether the movement occurs in an egocentric (Temprado et al., 2003, Experiment 2) or alocentric (Salesse, Oullier, & Temprado, 2005) frame of reference. Moreover, when visual perception is the only mediating factor of coordination pattern stability (i.e. between persons coordination), visual directional coupling takes precedence over the neuromuscular constraint (Salesse, Temprado, & Swinnen, 2005;

Temprado et al., 2003) by stabilizing the iso-directional movements. Thus it appears that directional and neuromuscular constrains are dissociable and depending on task context (i.e. plane of motion, Salesse et al., 2005) they may either cooperate or counteract each other to enhance or reduce the stability of intermanual coordination (Amazeen, DaSilva, & Amazeen, 2008). This dissociation of constraints and their context dependent nature has been shown during the coordination of both ipsilateral and heterolateral limbs coordination (Meesen, et al., 2006). For example, when non-isofunctional muscles are coupled, coordination accuracy is enhanced during iso-directional movements in extrinsic space. However, when isofuctional muscles are simultaneously activated, performance is more accurate compared with non-isofunctional muscle activation regardless of movement direction (Meesen et al., 2006; Salesse et al., 2005). Thus it appears that multiple constraints may coexist and there is evidence for combinability and exchangeability of these constraints. These are highly dependent on the nature of the task and environmental context in which specific coordination patterns are performed.

Perceptual aspects of bimanual coordination

The nature of non-linear coupling among the component oscillators that was represented in abstract mathematical terms (Haken et al., 1985; Schoner et al., 1986; Haken, Peper, Beek, & Daffertshofer, 1996) has also been repeatedly linked to the perceptual information available. For example research paradigms such as interpersonal coordination tasks (Schmidt et al., 1990), and unimanual tracking tasks (Wilson, Collins, & Bingham, 2005b), whereby a direct neuromuscular connection between oscillating components was not present, also exhibit stable coordination patterns at 0^{o} and 180^{o}

relative phase. These results suggest that coupling can occur at a perceptual level. Moreover, Bingham and colleagues (e.g., 1999; 2004a, b; Wilson, Collins, & Bingham 2005a, b) have argued that bimanual coordination can be limited by the performer's ability to detect a given relative phase pattern throughout visual perception. That is, if a participant rates a given observed pattern of behavior as uncoordinated and cannot distinguish the amount of variability in the pattern, then it is likely that they will not be able to produce the pattern. Consequently, the reason for poor performance in some bimanual tasks is that participants are unable to detect their errors and thus, are unable to initiate corrections. Using the same logic, the argument can be made that if perceptual information is provided that facilitates pattern detection then error detection (and correction) will follow allowing stable performance to be effectively tuned-in (Kovacs et al., 2009a). The work of Bingham and colleagues establishes a link between visual perception and the stability of symmetric and asymmetric coordination patterns. Similarly, Mechsner, Kerzel, Knoblich, & Prinz (2001) provided evidence that coordinated bimanual movements can be organized in terms of perceptual symmetry as well as motoric symmetry as previous work had shown (see Riek, Carson & Byblow, 1992 for opposite findings). That is, Mechsner et al. have shown that a bimanual coordination pattern in which the simultaneous activation of non-homologous muscles is required can be performed as stably as a coordination pattern requiring simultaneous activation of homologous muscles, provided the visual symmetry of movement direction. However, Mechsner's dichotomous view whereby coordinated movements are purely perceptual–cognitive/ psychological in nature (Mechsner, 2004) has been

intensively questioned by many scientists (e.g. Commentaries on F. Mechsner (2004), "A psychological approach to human voluntary movements" and response of the author).

Lissajous feedback

One method that has been used for some time (e.g., Kelso & Scholz, 1985) to display bimanual coordination data and show stability differences in patterns is the angle-angle plot or Lissajous plot. The Lissajous plot integrates the position of the two limbs into a single point in one plane by plotting the movement of one limb on the horizontal axis and plotting the movement of the other limb on the vertical axis. Additionally, when the Lissajous plot is overlaid on the same plane with a Lissajous template depicting a goal coordination pattern participants are able to detect and correct deviations from the goal coordination pattern. In attempts to provide integrated limb movement feedback in bimanual 1:1 and polyrhythmic coordination experiments, Lissajous plots have been used to provide concurrent and/or terminal feedback (e.g., Lee, Swinnen, & Verschueren, 1995; Summers, Davis, & Byblow, 2002; Swinnen et al, 1998; Swinnen, Lee et al, 1997; Swinnen, Dounskaia et al., 1997). However, even with the use of Lissajous feedback, extensive practice was still required to effectively produce coordination patterns other than in-phase or anti-phase (e.g., Lee, et al., 1995; Swinnen et al., 1998; Swinnen, Lee et al., 1997). On the other hand, Kovacs and colleagues (Kovacs et al., 2009a, b) using Lissajous plot feedback have recently shown that participants can effectively (relative phase error and variability levels around 10^{o}) perform continuous coordination patterns that traditionally required multiple days of practice, after only a limited (5 minutes) amount of practice. Kovacs and colleagues

argued that this level of performance was possible because distracting attentional demands in the environment (e.g. auditory or visual metronomes, vision of the limbs) were reduced allowing the participants to focus primarily on the concurrent feedback provided by the Lissajous plots. Indeed, previous studies that have used this same type of feedback have still required extensive practice to achieve stable performance because external pacing devices were used and/or vision of the limbs was permitted. In sum, it appears that unified and integrated perceptual information (Lissajous plot and template) allows participants to improve performance on bimanual coordination patterns that have traditionally been considered difficult to perform, provided that attentional distracters in the environment are reduced or eliminated.

CHAPTER III

EXPERIMENT 1- 1:1 BIMANUAL COORDINATION WITH DIFFERENT AMPLITUDES

Introduction

Bimanual coordination has been modeled as non-linearly coupled limit cycle oscillators (Haken et al., 1985) perturbed by stochastic forces (Schöner et al., 1986). An important characteristic of a system of coupled oscillators is that the individual components (oscillators/limbs) constantly interact, and thus influencing the individual behavior as well as the collective component. Many experiments have revealed that due to this interaction bimanual coordination patterns are inherently limited to the stable patterns of in-phase (relative phase between oscillating components, $\Phi = 0^{o}$) and anti-phase ($\Phi = 180^{o}$) (Tuller & Kelso, 1989; Yamanishi et al., 1980) while other patterns (e.g. $\Phi = 90^{o}$) cannot be performed without additional practice (Fontaine, Lee, & Swinnen, 1997; Swinnen, Lee et al., 1997, Zanone & Kelso, 1992, 1997).

The difficulty in performing other phase relations has typically been attributed to the attraction toward the intrinsic dynamics of in-phase and anti-phase (Schöner & Kelso, 1988), the instability associated with the activation of homologous and non-homologous muscles via crossed and uncrossed corticospinal pathways (Cattaert et al., 1999; Kagerer et al., 2003; Kennerley et al., 2002; for review see Swinnen, 2002) as well as the time delays associated with the integration of the afferent and efferent signals due to anatomical connectivity (Peper & Beek, 1999; Banerjee & Jirsa, 2006). Additionally, the coupling between limbs has been shown to be asymmetrical in that the dominant hand

exerts greater influence on the nondominant hand than vice-versa (DePoel, Peper, & Beek, 2007). Indeed, experimental evidence indicates that handedness and attentional focus directed to one or the other limb have a similar influence on the symmetry of the coupling between the components (e.g., Peters, 1989; Treffner & Turvey, 1995, 1996; Amazeen et al., 1997). For example, Amazeen et al. (1997) have provided evidence for handedness-related coupling asymmetry in a 1:1 frequency locked bimanual coordination task with left-handed participants tending to lead with their left hand while right-handed participants tended to lead with their right hand, (also see Treffner & Turvey, 1995, 1996). Additionally, the results of Amazeen et al. (1997) extend previous findings, indicating that attentional focus to one or the other limb is a mediating variable that influences asymmetric coupling between limbs. Peters (1989) suggested that the expression of handedness in bimanual coordination may be the reflection of an inherent attentional bias, with right-handed participants preferentially attending to their right limb and left-handed participants preferentially attending to their left limb. However, the results of Amazeen et al. (1997) indicate that the effects of an imposed attentional asymmetry are similar to those resulting from the intrinsic bilateral asymmetry (handedness), but this symmetry does not necessarily imply causality, suggesting that attention and handedness are related through their mutual effects on the bimanual coordination dynamics (for similar results see de Poel et al., 2008).

Another source of asymmetry in coupling strength which has received extensive experimental attention, is amplitude disparity between the movements of two limbs (e.g. Peper & Beek, 1998; Post, Peper, & Beek, 2000), whereby the limb moving at smaller

amplitude is more strongly influenced by the contralateral limb moving with a larger amplitude than vice versa (Peper et al., 2008). When two limbs are required to simultaneously perform movements of disparate amplitudes, spatial assimilation has been observed whereby the limb moving with the smaller amplitude tends to overshoot while the limb moving with the larger amplitude tends to undershoot. Amplitude assimilation (amplitude coupling) has been documented for discrete (Sherwood, 1994; Marteniuk, MacKenzie, & Baba, 1984) as well as continuous (Spijkers & Heuer, 1995; Buchanan & Ryu, 2006) bimanual movements. As early as 1980, Marteniuk & MacKenzie introduced a model of two-hand control in which they propose that the magnitude of amplitude coupling is directly related to the interlimb difference in amplitudes. In other words, the larger the amplitude disparity, the larger the interaction between the limbs. In an attempt to directly test the predictions of the Marteniuk & MacKenzie (1980) model, Sherwood (1994) found that amplitude assimilation occurs but only when amplitude difference is double, That is one limb has to move double the distance of the other (for similar results see Marteniuk et al., 1984). Additionally, in an experiment where participants had to perform bimanual continuous movements in the horizontal plane Spijkers & Heuer (1995) have found evidence of amplitude assimilation. It is noteworthy that in the Spijkers and Heuer experiment amplitude disparity was also double (10 and 20 cm). Not only was the amplitude related coupling found to be asymmetric in that the limb moving at the larger amplitude influenced more the limb moving at the smaller amplitude, but the coupling was found to be asymmetric in terms of handedness. In other words, for right handed participants, when the left limb

performed the smaller amplitude movement the increase in amplitude (Constant Error) was larger than when the right limb performed the smaller amplitude. Conversely, while performing the larger amplitude movement the left limb tended to undershoot to a lesser extent compared with the right limb (Sherwood, 1994; Marteniuk et al., 1984; Spijkers & Heuer, 1995). Furthermore, movement frequency and amplitude are inversely related, in that an increase in movement frequency is accompanied by a decrease in movement amplitude for externally paced (Beek, Rikkert, & van Wieringen, 1996) movements, as well as for movements performed at a preferred frequency (Rosenbaum, Slotta, Vaughan, & Plamondon, 1991). Alternatively, an asymmetry in movement amplitudes between the limbs may be inversely associated with a difference in preferred movement frequency (Ryu & Buchanan, 2004). Recent studies supporting this hypothesis indicate that a disparity in movement amplitude may influence the lead-lag relationship between limbs (Heuer & Klein, 2005; Buchanan & Ryu, 2006, de Poel, Peper, & Beek, 2009), where the limb performing the smaller amplitude tends to lead in time the limb performing the larger amplitude. Additionally, this lead-lag relation yielded phase relations that are slightly but systematically shifted away from the intended coordination patterns (Buchanan & Ryu, 2006). Thus, amplitude disparity seems to affect bimanual coordination at the collective level (relative phase) as well as at the component level (amplitude of individual limbs).

Although the exact neurophysiological sources of the interlimb interactions are still to be determined, candidate mechanisms and/or processes have been identified (for reviews see Carson, 2005; Swinnen, 2002) for which the strength of the neural signal

may be associated with the strength of coupling between the limbs. For example, it has been argued that enhanced neural activity (e.g. increased movement amplitude, increased load) increases the level of neural crosstalk at the level of cerebral hemispheres via the corpus callosum (Kennerley et al., 2002) and also at the spinal level via the ipsilateral corticospinal pathways (Preilowski, 1975; Kagerer et al., 2003), having a strong effect on the contralateral limb. Consistent with this expectation, Walter & Swinnen (1990) found that adding additional load to an arm that performs a reversal movement greatly influenced the contralateral arm performing a unidirectional movement, in that the latter had strong reversal tendencies. Although neurophysiological accounts (such as neural crosstalk) for the bimanual coordination dynamics emphasize constraints primarily related to the action component of the perception-action system, perceptual influences have also been shown to have a significant influence on the coordination dynamics (Kovacs et al., 2009a, b, c, in press; Zaal, Bingham, & Schmidt, 2000; Swinnen, Lee et al., 1997; Bingham, 2004a). In a series of recent experiments Kovacs and colleagues (Kovacs et al., 2009a, b, c, in press) have demonstrated that certain coordination patterns that have been deemed difficult or almost impossible to perform, can if fact be performed quite easily provided attentional demands in the testing environment are substantially reduced (e.g., no external pacing, vision of the limbs is not allowed) and movement feedback is provided in a very specific way (Lissajous plots) that facilitates error detection and allows corrections to be made easily. The Lissajous plots integrates the position of the two limbs into a single point in one plane by having the movement of one limb move the cursor horizontally while the motion of the other limb moves the

cursor vertically. Lissajous feedback has been used to provide concurrent (e.g. Amazeen et al., 2008; Swinnen, Lee et al., 1997; Lee et al., 1995) and/or terminal (e.g. Hurley & Lee, 2006; Swinnen, Verschueren et al., 1998) feedback information to the performer in bimanual experiments requiring individuals to learn novel 1:1 coordination patterns with various phase lags (e.g. Kovacs et al., 2009a, b) and multi-frequency coordination patterns (e.g., Summers et al., 2002; Swinnen, Dounskaia et al., 1997; Kovacs et al., 2009c, in press). For example, Kovacs and colleagues (Kovacs et al., 2009a, b) have demonstrated that participants can produce with low error and variability relative phase patterns between 0^o and 180^o relative phase (Yamanishi et al., 1980; Zanone & Kelso, 1992) with very little practice when provided salient integrated feedback (Lissajous plots) and other perceptual (vision of the limbs) and/or attentional distractions (metronome) were reduced. Note that the difficulty in producing relative phase patterns other than in-phase and anti-phase has typically been attributed to phase attraction that draws the coordination between the limbs toward the intrinsic dynamics (Schöner & Kelso, 1988) and/or the instability associated with neural cross-talk during the activation of homologous and non-homologous muscles via crossed and un-crossed cortico-spinal pathways (Kennerley et al., 2002). In the Kovacs et al. (2009b) experiment participants produced relative phase patterns between 30^o and180^o with remarkably low levels of error (~10^o) and variability (~10^o) with only the in-phase pattern (0^o relative phase) having lower error and variability (~4^o-5^o). In other words, what the Kovacs and colleagues experiments demonstrate is that the difficulty in performing certain

coordination patterns is attributable to a certain degree to perceptual and attentional factors present in the testing environment.

The main purposes of the present experiment were to determine if salient perceptual feedback and reduced attentional demands in a 1:1 bimanual coordination task might alter the coordination dynamics of the two limbs moving at different amplitudes and more importantly whether the dynamics of the individual components (limbs) might change due to changes in the perceptual information provided during performance. For a given movement time, an increase in movement amplitude requires an increased movement velocity, which in turn can be achieved by increasing the magnitude of contraction forces. An increase in contraction forces is associated with an increase in the strength of the neural signal. It is likely that enhanced neural activity leads to stronger contralateral effects due to increased neural crosstalk via the corpus calossum (Kennerley et al., 2002) and ipisilateral corticospinal pathways (Kagerer et al., 2003). Based on the notion of increased crosstalk due to increased neural activity induced by the amplitude disparity, it would be expected that in a testing condition in which salient integrated feedback is not provided, amplitude assimilation would occur. In other words, if for example the limbs are to perform rhythmical movements, and the left limb is required to move at half the amplitude of the right limb, it would be expected that the left limb will increase its amplitude while the right limb will decrease its amplitude compared to a required amplitude. However, if amplitude assimilation is not primarily resulting from crosstalk, but arises in part from perceptual-attentional demands present in the testing environment, it would be expected that providing salient integrated

feedback (Lissajous plot) would reduce this effect. Moreover, consistent with the idea that coupling between the dominant and nondominant limbs is asymmetric (Peper et al., 2008) amplitude assimilation has also been found to be asymmetric depending on which limb performs the larger amplitude (e.g. Marteniuk et al., 1984; Buchanan & Ryu, 2006). Therefore, in the present experiment, it was expected that the presentation of Lissajous feedback would have a greater effect when the dominant (right) limb performs the larger amplitude.

Method

Participants

College students (N=20) received academic credit for participation in the experiment. The participants had no prior experience with the experimental task and were informed of the specific purpose of the study. Participants were strong right-hand dominant (mean laterality quotient [LQ] = 79) as determined by the Edinburgh handedness inventory (Oldfield, 1971). Informed consent approved by the IRB for the ethical treatment of experimental participants at Texas A&M University was obtained prior to participation in the experiment.

Apparatus

The apparatus consists of two horizontal levers and a projector. The levers were affixed at the proximal ends to near frictionless vertical axles. The axles, which rotated freely in ball-bearing supports, allowed the levers to move in the horizontal plane over the table surface. Near the distal end of each lever, a vertical handle was attached. The positioning of the handle was adjustable. When the participant rested their forearm on

the lever with their elbow aligned over the axis of rotation the position of the handle was adjusted so they could comfortably grasp the handle (palm vertical) (Figure 1A). The participant's limbs were covered throughout the experiment. The horizontal movement of the levers was monitored (200 Hz) by potentiometers that were attached to the lower ends of the axles.

Procedure

All participants were informed that they had to attempt to flex and extend their left and right limbs about the elbow in order to produce the desired amplitude and relative phase relationship. Participants were assigned to a Lissajous or no-Lissajous condition prior to entering the testing room. In the Lissajous condition on-line data was used to project a cursor (small circle) on a screen directly to the front of the participant with the position of the left lever moving the cursor up (extension) and down (flexion). The movement of the right lever resulted in moving the cursor left (flexion) and right (extension). Also projected onto the screen was one of the Lissajous plots that represented a 1:1 pattern of continuous sinusoidal motion with the required relative phase for that trial (Figure 1C). The current position of the limbs was indicated by the cursor overlaid on the template with the participant's goal defined as moving the cursor in a way to match the general shape of the Lissajous template projected on the screen in front of them. In the no-Lissajous condition, two horizontal line pairs were projected on the screen representing the target amplitudes. Two horizontal blue lines represented the target amplitudes for the left limb while two horizontal red lines represent the target amplitude of the right limb (Figure 1B). The current position of the participant's limbs

was indicated by a blue (left limb) and a red (right limb) cursor. The movement of the left and right levers resulted in moving the corresponding cursors up (extension) and down (flexion). Participants in the no-Lissajous group were instructed to move the cursors between the corresponding target pairs. It was emphasized that the movements of both limbs should be continuous. After each trial, in which the cycling frequency of the limbs was below 1Hz, the experimenter encouraged the participants to increase their movement speed without disrupting the intended movement pattern. Participants were informed that Blocks 1-3 are considered training blocks and only data from Block 4 was to be retained for further analysis. All participants were required to perform three 1:1 phase relationships: 0^o relative phase (in-phase), 90^o relative phase and 180^o relative phase (anti-phase) in the following serial schedule: $0^o – 90^o – 180^o – 180^o – 90^o – 0^o$.

Participants in the no-Lissajous condition were instructed that during in-phase coordination the cursors corresponding to the right and left limb displacement should reach simultaneously the two lower and the two upper target lines representing the amplitude for each limb. Similarly, during anti-phase coordination when one of the cursors reached the lower target line, the cursor representing the opposite limb's displacement had to reach the upper target line. In order to achieve the 90^o relative phase coordination pattern, participants were explained that one of the limbs should always be half way through the motion cycle when the opposite limb reaches the lower or the upper target line.

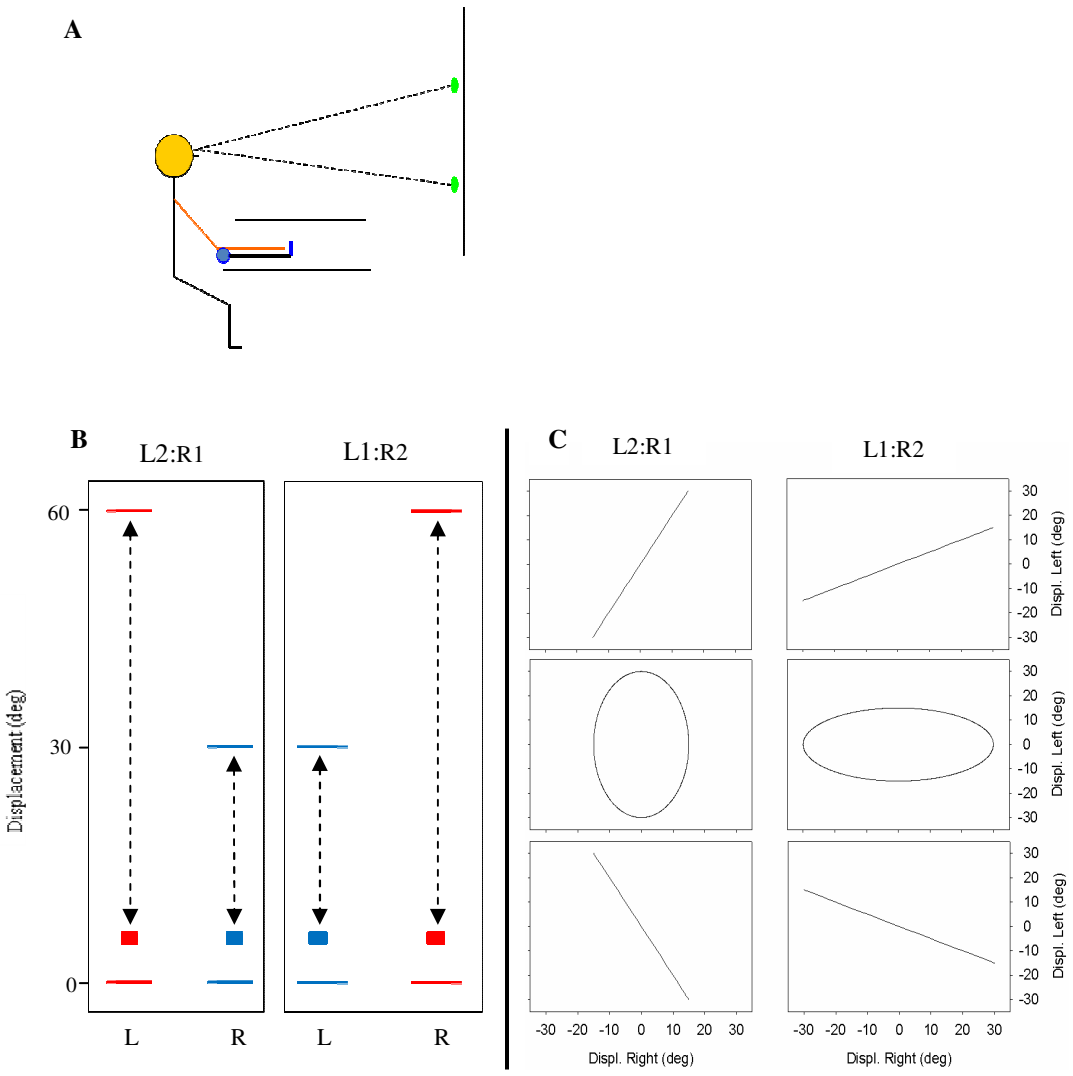

Figure 1. View of the set-up for Experiment 1. Illustration of the experimental setup (A) and the visual feedback provided during the experiment for the no-Lissajous group (B) and the Lissajous group (C) under both amplitude conditions (see text for detailed explanation).

Each relative phase was performed for 30 seconds. This schedule was repeated two times within a block: first with the left limb moving at twice the amplitude of the right (L2:R1) and, second with the right limbs moving at twice the amplitude of the left (L1:R2), counterbalanced between participants. The corresponding movement amplitude was 60^{o} for the limb moving at the larger amplitude and 30^{o} for the limb moving at smaller amplitude.

Measures and data reduction

All data reduction was performed using MATLAB. The potentiometer signals representing the limbs' displacements were low-pass filtered with a second order dual pass Butterworth with a cutoff frequency of 10 Hz. Velocity signal was computed with the displacement signal filtered (Butterworth, 10 Hz) before performing the differentiation. The analyses was focused on both bimanual coordination performance of the required phase relationship and unimanual motion performance of the right and left limbs.

Bimanual measures

To examine the spatial-temporal coordination of the limbs' motion, the continuous relative phase (ϕ) between the two limbs was computed. Prior to computation of the continuous relative phase, displacement and velocity data for each limb was normalized in two steps. First the mean of each data series was subtracted from each data point in the series to mean center the time series around zero. Second, amplitude rescaling was done by dividing the positive and negative amplitudes with the maximum positive or negative amplitude value. The phase angle (θ_i) for each limb ($i = r, l$) was computed for

each sample of the displacement time series using the following formula adapted from Kelso et al. (1986):

$$\theta_i = tan^{-1}[(dX_i/dt)/X_i]$$

with X_i representing normalized limb position and dX_i/dt normalized instantaneous velocity. Next, the continuous relative phase was computed by subtracting the phase angle of the left limb (θ_l) from the phase angle of the right limb (θ_r), $\phi = \theta_r - \theta_l$. Root mean square error ($RMSE_{rph}$) of the continuous relative phase was used as a measure of the degree to which the goal relative phase (e.g. 90°) was achieved. The standard deviation (VE_{rph}) of the performed relative phase was used as a measure of stability of the performed pattern and, the constant error of relative phase (CE_{rph}) was used as a measure for the lead-lag relationship of the two limbs performing the coordination task.

Unimanual measures

Using the time series of displacement that was mean centered around zero, cycle duration was computed on a cycle basis with each cycle representing every other zero crossing (Z_C) in the displacement trace (Cycle duration = Z_{Ci+2} - Z_{Ci}). To examine the attainment of the required amplitude for each limb, the mean amplitude was computed for each trial. Next, constant error of amplitude (CE_{amp}) was computed for each limb as the signed error from the target amplitude. A positive constant error would indicate that the limb was overshooting (higher amplitude) while a negative error would indicate that the limb was undershooting the required amplitude.

Results

Root mean square error ($RMSE_{rph}$), constant error (CE_{rph}) and variability (VE_{rph}) of the performed relative phase were analyzed in a 2 Group (Lissajous, no-Lissajous) x 2 Amplitude condition (L2:R1, L1:R2) x 3 Goal phase (0^o, 90^o, 180^o) ANOVAs with repeated measures on amplitude condition and goal phase. These results are presented in the bimanual performance section. Mean cycle duration and constant error of individual limb amplitudes (CE_{amp}) were analyzed in a 2 Group (Lissajous, no-Lissajous) x 2 Limb (Left, Right) x 2 Amplitude condition (L2:R1, L1:R2) x 3 Goal phase (0^o, 90^o, 180^o) ANOVAs with repeated measures on limb, amplitude condition and goal phase. These measures are presented in the unimanual performance section. Duncan's new multiple range test and simple main effect post-hoc tests were performed when appropriate (α = 0.05).

Bimanual performance

The analysis of $RMSE_{rph}$ of relative phase detected a main effect of Goal phase, $F_{(2,36)} = 7.57$, $p < 0.01$, with Duncan's new multiple range test indicating that $\phi = 90^o$ was produced with more error than $\phi = 0^o$ and $\phi = 180^o$ which were not different from each other. The main effect of Group, $F_{(1,18)} = 11.01$, $p < 0.01$, as well as the Group x Amplitude condition interaction, $F_{(1, 18)} = 18.17$, $p < 0.01$ were also significant. Simple main effect analysis indicated that the Lissajous group performed the task with less error compared with the no-Lissajous group under both amplitude conditions, suggesting that participants in the Lissajous group were able to more closely match the required relative phase (Figure 2).

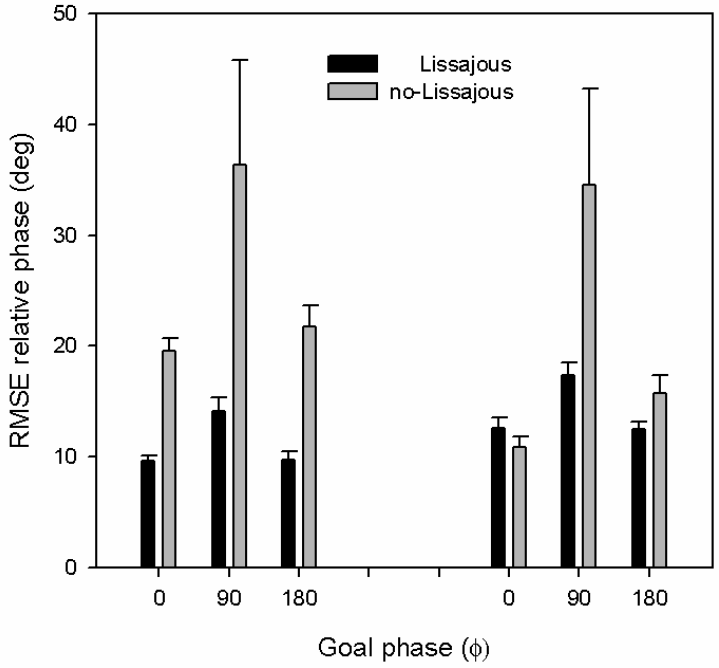

Figure 2. RMS error of relative phase. $RMSE_{rph}$ for participants in the Lissajous and no-Lissajous groups. Results are grouped by the goal relative phases and by the amplitude conditions. Error bars represent the standard error of the mean.

Additionally, no difference in $RMSE_{rph}$ was found between the two amplitude conditions for the Lissajous group, but a difference was found for the no-Lissajous group which produced lower error under the L1:R2 amplitude condition (M=20.36 deg, S_{EM}=3.43 deg) compared with the L2:R1 condition (M=25.88 deg, S_{EM}=3.42 deg).

In terms of constant error of relative phase (CE_{rph}), a measure of the lead-lag relationship between limbs, the analysis detected a main effect of Goal phase, $F_{(2,36)} = 8.26$, $p < 0.01$, with Duncan's new multiple range test indicating more bias (higher CE_{rph}) when producing $\phi = 90^{o}$ and $\phi = 0^{o}$, which were not different from each other, and

less bias when producing $\phi = 180^{o}$. The main effect of Group was also significant, $F_{(1,18)} = 4.83$, $p < 0.05$, with the Lissajous group having less bias compared to the no-Lissajous group (Figure 3). The Group x Amplitude condition interaction failed to reach significance, $F_{(1,18)} = 3.30$, $p < 0.08$, but gives an indication relative to the lead-lag tendencies of the individual limbs under the different Amplitude conditions.

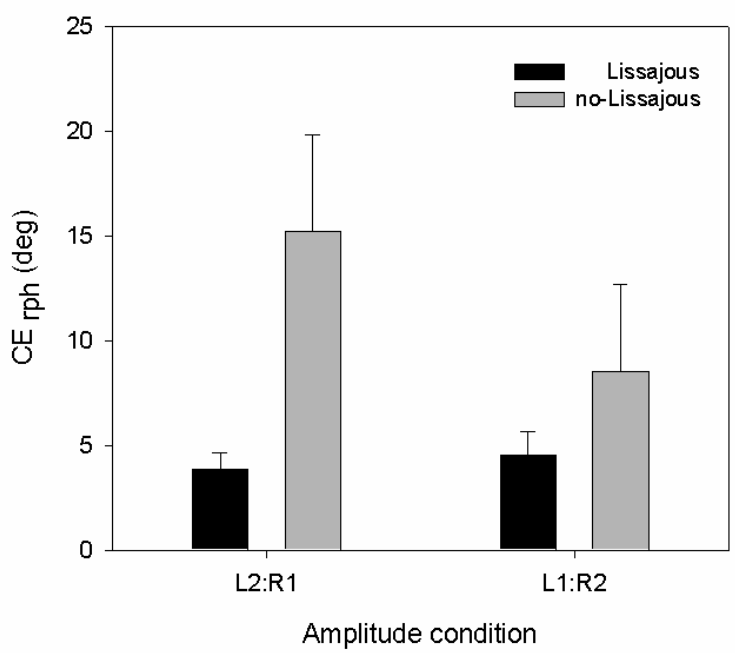

Figure 3. Constant error of relative phase. CE_{rph} for participants in the Lissajous and no-Lissajous groups. Results are grouped by the amplitude conditions. Error bars represent standard error of the mean.

The ANOVA on relative phase variability (VE_{rph}) detected a main effect of Goal phase, $F_{(2,36)} = 128.11$, $p < 0.01$, with Duncan's new multiple range test indicating that performance at $\phi = 90^{o}$ was more variable than performance at $\phi = 180^{o}$, which in turn

was more variable than performance at $\phi = 0^{o}$. The main effect of Amplitude condition, $F_{(1,18)} = 9.25$, $p < 0.01$, as well as the Group x Amplitude condition interaction, $F_{(1, 18)} = 5.34$, $p < 0.05$, were also significant. Simple main effect analysis indicated that performance of the Lissajous group was less variable (M=9.47 deg, S_{EM}=0.72 deg) compared with that of the no-Lissajous group (M=12.19 deg, S_{EM}=0.74 deg) under the L2:R1 amplitude condition but not different under the L1:R2 condition. Additionally, no difference in variability was found between the two amplitude conditions for the no-Lissajous group, but a difference was found for the Lissajous group which had lower variability of relative phase under the L2:R1 amplitude condition (M=9.47 deg, S_{EM}=0.72 deg) compared with the L1:R2 condition (M=11.8 deg, S_{EM}=0.85 deg.) (Figure 4). All other interactions in the bimanual measures failed to reach significance.

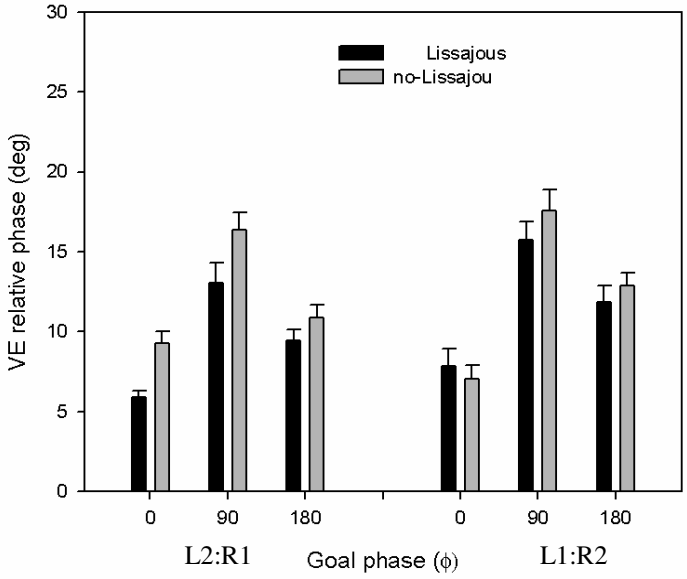

Figure 4. Variability of relative phase. VE_{rph} for participants in the Lissajous and no-Lissajous groups. Results are grouped by the goal relative phases and by the amplitude conditions. Error bars represent standard error of the mean.

Unimanual performance

The analysis of the mean cycle duration data failed to detect a difference between the Lissajous and no-Lissajous groups $F_{(1,18)} = 1.84$, $p > 0.1$, as well as between the right and left limbs $F_{(1,18)} < 1$, $p > 0.1$. However, the analysis did detect a main effect of Amplitude condition $F_{(1,18)} = 19.2$, $p < 0.01$ indicating that participants in general had shorter cycle durations under the L2:R1 condition (M = 989 ms, S_{EM} = 5.65 ms) compared with the L1:R2 condition (M = 1030.75 ms, S_{EM} = 5.75 ms). Similarly, the analysis detected a main effect of Goal phase $F_{(2,36)} = 7.07$, $p < 0.01$, with Duncan's new multiple range test indicating longer cycle duration while performing at $\phi = 90^{o}$ (M = 1034.3 ms, S_{EM} = 7.65 ms) pattern compared with the $\phi = 0^{o}$ (M = 998.95 ms, S_{EM} = 7.6 ms) and with the $\phi = 180^{o}$ (M = 995.6 ms, S_{EM} = 7.8 ms) patterns which were not different from each other. On average, participants in both groups performed the cyclical movements at the required frequency (1Hz) and had similar profiles of cycle durations across all conditions. Therefore this aspect will not be further addressed in the discussion section.

The main measure of interest for unimanual measures was the constant error (CE_{amp}) of displacement for each limb. A negative value for CE_{amp} of the limb performing at the larger amplitude and/or a positive value of CE_{amp} for the limb performing at the smaller amplitude would indicate an amplitude assimilation effect that exerts an attraction in amplitude of the two limbs. The ANOVA detected a main effect of Goal phase, $F_{(2,36)} = 3.96$, $p < 0.05$, with higher constant error during the anti-phase ($\phi = 180^{o}$) coordination

pattern (M = 1.18 deg, S_{EM} = 0.26 deg) compared with the $\phi = 90^{o}$ coordination pattern (M = 0.65 deg, S_{EM} = 0.28 deg).

The ANOVA also detected a main effect of Limb, $F_{(1,18)} = 170.4$, $p < 0.01$ as well as a significant Limb x Amplitude condition, $F_{(1,126)} = 381.36$, $p < 0.01$, interaction. Simple main effect analysis detected significant differences between the left and right limbs under the L1:R2 amplitude condition with the left limb overshooting (M=3.35 deg, SEM=0.26) and the right limb undershooting (M= -1.39 deg, SEM=0.2) the target amplitude. Also the amplitude bias of the left limb was significantly higher under the

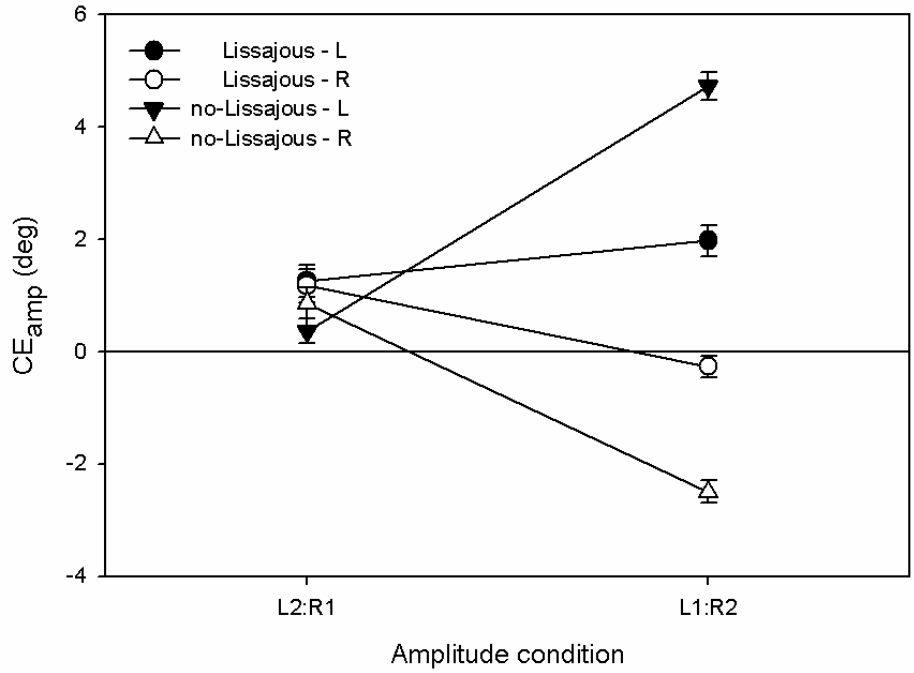

Figure 5. Amplitude assimilation. CE_{amp} for the right and left limbs of participants in the Lissajous and no-Lissajous groups. Results are grouped by the amplitude conditions. Error bars represent standard error of the mean.

L1:R2 (M=3.35, SEM=0.26) compared with the L2:R1 amplitude condition (M=0.81, SEM=0.18). Similarly, the amplitude bias of the right limb was significantly different under the L1:R2 (M= -1.39 deg, SEM=0.2) compared with the L2:R1 (M=1.01, SEM=0.19) amplitude condition.

The Group x Limb, $F_{(1,18)} = 40.1$, $p < 0.01$, Group x Amplitude, $F_{(1,18)} = 4.75$, $p < 0.05$, and Group x Limb x Amplitude, $F_{(1,126)} = 120.69$, $p < 0.01$, interactions were also significant (Figure 5). The simple main effect analysis indicated that participants in the Lissajous group had less bias with their left (M=1.61 deg, SEM=0.2) and right (M=0.44 deg, SEM=0.19) limb compared with the left (M=2.54, SEM=0.32) and right (M= -0.82, SEM=0.27) limbs of the no-Lissajous group. Simple main effect analysis failed to detect difference between the Lissajous and no-Lissajous groups under the two amplitude conditions.

Discussion

The present experiment was designed to examine how salient perceptual feedback in the form of a Lissajous plot and template influences the amplitude assimilation between two limbs during a rhythmic bimanual coordination task that requires each limb to perform a movement with different amplitude. Participants coordinated rhythmic movements of their forearms while being provided separate feedback for each limb (no-Lissajous group) or integrated feedback (Lissajous group). Attentional demands were reduced by allowing participants to self-pace their cyclical movements (no external pacing metronome) while also blocking vision of the limbs which has also been shown to have a disrupting effect on successfully performing a bimanual coordination task

when Lissajous feedback is provided (Kovacs et al., 2009a, b, c). The task was to maintain a 0^0 (in-phase), 180^0 (anti-phase) or 90^0 phase relationship between limbs while also matching the required disparate amplitudes for each limb. By comparing the amplitude bias (CE_{amp}) of each limb under different conditions it was possible to determine the degree of amplitude assimilation exerted by what has been termed the asymmetric coupling between the limbs. Note that, amplitude disparity between coordinating limbs has been shown to have distinct effects on the behavior at the collective level (performed relative phase) as well as at the individual component (limbs) level. These aspects will be discussed next.

Effects at the collective level

As expected based on previous results (Kovacs et al., 2009a, b), participants in the Lissajous group were quite successful in achieving the required coordination patterns ($\Phi = 0^o$, $\Phi = 180^o$, and $\Phi = 90^o$) under both amplitude conditions (Figure 2). Variability (VE_{rph})of relative phase and $RMSE_{rph}$ of relative phase (~ 12^o) of participants in the Lissajous group, although comparable, were slightly increased (~ 4^o) compared with our previous experiments using the same experimental setup (Kovacs et al., 2009 b). A potential source for the observed increase in relative phase $RMSE_{rph}$ and variability could be the fact that in the present experiment the amplitudes of the oscillating limbs were not equal. Asymmetry in movement amplitudes between the limbs has been found to be inversely associated with movement frequency (Beek et al., 1996) such that large movement amplitudes are related to low preferred oscillation frequencies. A difference between the preferred oscillation frequencies, in turn, can influence the relative phasing

between limbs such that the limb with the higher preferred frequency tends to lead the limb with the lower preferred frequency (Buchanan & Ryu, 2006; de Poel et al., 2009). This yields a slight but systematic shift away from the intended phase relation (Fuchs, Jirsa, Haken, & Kelso, 1996). In the Lissajous condition however, this systematic shift might have been corrected soon enough to only yield minor (~ 3^{o}) deviations from the intended phase relation. Note that one of the advantages of the Lissajous template and the overlaid real-time Lissajous plot is that it provides in the same plane the to-be-performed template and the actual performed pattern, so that error detection and subsequent corrections are facilitated.

In the no-Lissajous condition, however, relative phase $RMSE_{rph}$ and variability were substantially higher compared with the Lissajous group, especially under the L2:R1 amplitude condition. While such high levels of $RMSE_{rph}$ for the no-Lissajous group might be expected for coordination patterns of $\Phi = 90^{o}$ (Kovacs et al., 2009b), it is quite surprising that $RMSE_{rph}$ levels were so elevated when performing in-phase coordination under the L2:R1 amplitude condition. Previous research using similar experimental setting (Kovacs et al., 2009b) found no differences between a Lissajous and no-Lissajous group when performing in-phase coordination pattern with equal amplitudes. In the present experiment however, the disparate amplitudes might have accentuated the drift of the actual relative phase pattern from the required pattern. Such results have been reported for example by Buchanan & Ryu (2006) using circle tracing tasks and Heuer & Klein (2005) using linear movements. In the Buchanan & Ryu experiments participants had to trace circle pairs of different diameters with their right and left limb either in in-

phase or anti-phase coordination pattern. Their results indicated consistent shift from the required fixed point values of 0^o and 180^o and the larger the difference in circle diameters the larger the shift (for similar results but different task see de Poel et al., 2009). Additionally these shifts were consistent with the expected lead-lag relation between limbs based on which limb was tracing the circle with the smaller diameter.

In the present experiment CE_{rph} of relative phase was not found to be significantly different between the two amplitude conditions for the Lissajous or no-Lissajous group. Values of CE_{rph} were positive under both amplitude conditions, indicative that the dominant right limb was always leading the non-dominant left limb. However, as presented in Figure 2C, there appears to be a tendency for the right limb to decrease the lead when the left limb is performing the smaller amplitude (L1:R2 condition) in the no-Lissajous group. Conversely, there is an increase of the right limb lead when the right limb is performing the movement with the smaller amplitude. Interestingly however, this tendency is not present in the Lissajous group. While CE_{rph} for the Lissajous group was greatly reduced compared to the no-Lissajous group, the lead of the right limb, in the Lissajous group, was similar in magnitude under the two amplitude conditions. It appears that the availability of the Lissajous plot, allowed participants to detect and correct deviations of relative phase from the intended pattern. Such deviations were not found in our previous work where amplitudes were the same. Although contrary to the prediction that the limb performing the smaller amplitude should lead the limb performing the larger amplitude, the results can be interpreted in light of previous experiments that have reported similar findings (Swinnen, Jardin, & Meulenbroek, 1996;

Amazeen et al., 1997; Amazeen, Ringenbach, & Amazeen, 2005). The Swinnen et al. (1996) experiment, for example, found consistent right limb lead for right handers in a circle tracing task. Although in the Swinnen et al experiment there was no disparity between the target amplitudes, the consistent right hand lead has been attributed to manual dominance and attentional bias. They found that attentional bias modulated the magnitude of the dominant (right) limb lead in a similar pattern as did amplitude disparity in the present experiment. More specifically, in the Swinnen et al experiment, when participants directed their attention to the right limb, the right hand lead increased compared to when attention was directed to the non-dominant (left) limb. In a more recent experiment, de Poel et al., (2009), have argued however that not attention manipulation (i.e. directing attention to one or the other limb) per se influences the lead-lag relationship between limbs, but rather attention modulates an increase in amplitude of the attended limb. In other words, the attended limb tends to increase its movement amplitude and as such influencing the relative phasing between limbs. In the present experiment directing attention to one or the other limb was not manipulated per se, in fact it was attempted to reduce as much as possible attentional demands by covering the limbs and not providing external pacing signals. These two factors have been shown to have detrimental effects on the performance of bimanual coordination patterns (Kovacs et al., 2009a, b, c). However, it might be possible that participants involuntarily directed their attention more or less towards one of their limbs. Indeed, the present set of results at the collective level (relative phase) suggest that participants in the no-Lissajous

condition might have directed their attention predominantly toward their right limb, and more so when they performed under the L2:R1 amplitude condition.

Effects at the component level

The main question of interest at the individual limb level was whether the limb moving at the smaller amplitude would overshoot and/or the limb moving at the larger amplitude would undershoot the target amplitudes as a result of asymmetric coupling between the limbs. In terms of the constant error of movement amplitude, the left limb on average performed at a higher than required amplitude (overshoot) while the right limb in general undershot the required amplitude. However, this effect was not consistent across the different amplitude conditions. The results show an asymmetric pattern in terms of amplitude bias, with both limbs overshooting under the L2:R1 condition but not under the L1:R2 condition (Figure 3). This pattern of results was similar for the Lissajous and no-Lissajous groups. Therefore amplitude assimilation will be discussed in terms of the general asymmetry between the L2:R1 and the L1:R2 conditions as well as the effect of the Lissajous feedback under the L1:R2 condition.

First, the pattern of results under the L1:R2 amplitude condition confirms the initial predictions. That is, when the dominant right limb performed the larger amplitude, the left limb tended to overshoot while the right limb tended to undershoot the required target amplitude. Moreover, amplitude bias was more pronounced for the left limb in that the left limb overshot to a greater extent than did the right limb undershoots. This asymmetry in amplitude assimilation is consistent with the notion that interlimb coupling strength scales with movement amplitude, with the limb performing the larger amplitude

influencing to a greater extent the limb moving at the smaller amplitude than vice versa. Indeed, several experiments reported similar findings using bimanual discrete aiming movements (Sherwood, 1994; Marteniuk et al., 1984; Weigelt & de Oliveira, 2003) or rhythmic cycling movements (Spijkers & Heuer, 1995; Peper et al., 2008; Amazeen et al., 2005; Buchanan & Ryu, 2006). This asymmetric amplitude assimilation was more pronounced for the no-Lissajous group compared with the Lissajous group. In other words participants in the Lissajous group overshot with their left limb and undershot with their right limb to a lesser extent than participants in the no-Lissajous group (Figure 3). It appears that the availability of the integrated Lissajous feedback allowed participants to more accurately monitor their performance and errors and initiate subsequent corrections. Indeed, the Lissajous plot integrates the displacement of both limbs into a single point, which hypothetically makes it easier to visually track and detect any deviations from the intended displacement. On the other hand, participants in the no-Lissajous group had to constantly monitor the amplitude accuracy of two limbs, much as in a bimanual Fitts task (Riek, Tresilian, Mon-Williams, Coppard, & Carson, 2003), which might have caused a constant shift of attention between the two limbs or the preferential allocation of attention to one of the limbs. For example, Spijker & Heuer (1995) have reported similar effects on amplitude assimilation, caused by both the amplitude disparity and the preferential focus of attention to one of the limbs. Moreover, in a recent experiment Shea & Kovacs (2009) have reported that during a discrete bimanual aiming task, the availability of Lissajous feedback greatly reduced the coupling in timing between limbs, but this effect was not observed for a group that was

not provided Lissajous feedback. It is important to note that in the present and most of the previous experiments, required amplitude manipulations were also confounded with spatial constraints, that is with fixed point locations where amplitude reversal had to be performed. This might have contributed to why participants preferentially direct their attention to the larger amplitude movement (the more difficult one) while allowing higher error (overshoot) of the limb performing the smaller amplitude. Indeed, de Poel et al. (2009) addressed this question using a bimanual cyclical movement of disparate amplitudes in which they solely manipulated the required movement amplitudes, rather than other spatial features of performance (e.g. fixed spatial location for movement reversal). Their results show that the overshooting and undershooting of the required amplitudes was similar for the two limbs when amplitude disparity was not spatially constrained.

Second, somewhat unexpectedly, the amplitude bias observed under the L2:R1 condition was quite different from that observed under the L1:R2 condition. Participants in both the Lissajous and no-Lissajous group overshot the required amplitude with both limbs when the left limb was performing the larger amplitude. While an increase in amplitude of the limb performing the smaller amplitude (right) was expected, an overshoot of the limb performing the larger amplitude (left) was not. Thus clearly amplitude assimilation did not occur in this condition. In spite of several reports of assimilation effect their absence is not a unique result (e.g., Heuer & Klein, 2006; Marteniuk et al., 1984). For example in the Marteniuk et al. experiments participants were required to perform rapid bimanual aiming movements of either same or disparate

amplitudes (amplitudes of 10 and 30 cm respectively). Their results indicate that amplitude assimilation occurred only when the right hand was performing the longer amplitude but not when the left hand performed the longer amplitude. In fact, when the left hand was assigned the larger amplitude, both hands overshot the target amplitude, similar to the results in the present experiment under the L2:R1 condition. Similarly, Heuer & Klein (2006) found no evidence of amplitude assimilation. Although the failure to find amplitude assimilation has not been discussed in these manuscripts, the question of why this occurs under one (L1:R2) but not under the other (L2:R1) condition is quite challenging. Some of the common factors across experiments and/or conditions that failed to demonstrate amplitude assimilation is that all participants were right hand dominant and attention focus to one or the other limb was not controlled for. Although the present experiment does not provide direct evidence, it seems plausible to consider the possibility that inherent interlimb asymmetry (handedness) might interact with attentional focus preferentially directed towards one or the other limb (or shifting between the two), and such differentially affect interlimb interaction in terms of amplitude assimilation.

In sum, the present set of data supports the notion that the lead-lag relationship as well as amplitude assimilation between limbs can be partially attributed to the visual perceptual factors present in the testing environment and, when provided a salient visual feedback these factors can be reduced or eliminated.

CHAPTER IV

EXPERIMENT 2- LEARNING OF A BIMANUAL 1:1 COORDINATION PATTERN WITH 90^{O} CONTINUOUS RELATIVE PHASE: FEEDBACK FREQUENCY

Introduction

Bimanual movements have been used extensively in the study of interlimb coordination, especially with respect to developing theories of temporal order. Researches employing a large number of experimental tasks have revealed remarkable temporal constraints (Kelso & deGuzman, 1988) that limit spontaneous bimanual coordination to two relatively stable patterns. Coordination patterns of in-phase (relative phase between oscillating components, $\Phi = 0^{o}$) and anti-phase ($\Phi = 180^{o}$) have repeatedly been found to be inherently more stable and easy to perform without extended practice. Other coordination patterns (e.g. $\Phi = 30^{o}$ - 150^{o}) are quite difficult to perform and require more practice in order to achieve relatively stable performance (Zanone & Kelso, 1992; Yamanishi et al., 1980). In other words, relative phase patterns other than in-phase and anti-phase are not inherently stable and when trying to perform coordination patterns with other phase relations, the motor system shows a bias towards what has been labeled the intrinsic dynamics of in-phase and anti-phase coordination (Schöner & Kelso, 1988). The difficulty in performing other phase relations has typically been attributed to the attraction toward the intrinsic dynamics of in-phase and anti-phase (Schöner & Kelso, 1988), the instability associated with the activation of homologous and non-homologous muscles via crossed and uncrossed corticospinal

pathways (Cattaert et al., 1999; Kagerer et al., 2003; Kennerley et al., 2002) as well as the time delays associated with the integration of the afferent and efferent signals due to anatomical connectivity (Peper & Beek, 1999; Banerjee & Jirsa, 2006).

Recent experiments however, have demonstrated that changes in the perceptual information available in the testing environment can greatly influence bimanual coordination, e.g., stabilize anti-phase and destabilize in-phase coordination patterns by changing the orientation of the hand (Mechsner et al., 2001). Moreover, in recent experiments Kovacs and colleagues (Kovacs et al., 2009a, b) have demonstrated that when attention splitting features of a task are greatly reduced (i.e. visual or auditory metronome, vision of the limbs) and a salient integrated visual feedback is provided (Lissajous plot and template), perception can free the perception-action system from constraints that typically limit it to the bi-stable regime of the intrinsic dynamics. For example, participants in the Kovacs et al. (2009a) experiment were asked to perform a 1:1 bimanual coordination task with a 90^{o} relative phase while receiving concurrent Lissajous feedback in the form of a cursor representing the joint position of the two limbs overlaid on the Lissajous template depicting the required phase relation between the limbs. The results showed that participants were quite effective in performing the required coordination pattern after only 5 minutes of practice when an auditory metronome was not used and vision of the limbs was not permitted. Similarly, Kovacs et al. (2009b) have demonstrated that when provided the Lissajous feedback participants can perform various 1:1 coordination patterns between 30^{o} – 150^{o} relative phase after only 4 minutes of practice at each relative phase with patterns of relative phase error and

variability substantially reduced to levels observed in previous experiment only after multiple days of practice, and then only for the relative phase pattern that was practiced (Zanone & Kelso, 1992). In contrast, participants that were paced by a visual metronome and allowed vision of their limbs had much poorer performance. Although Lissajous plots have been used in a number of bimanual coordination experiments, results showed only moderate success compared with those reported by Kovacs and colleagues. That is, even with concurrent Lissajous information provided 1:1 bimanual coordination patterns with 90^{o} relative phase requires several days of practice for this coordination pattern to be produced with relatively small relative phase error and variability (e.g., Hurley & Lee, 2006; Lee et al., 1995; Swinnen et al., 1997a, b). Typically in these experiments external pacing devises were used and/or vision of the limbs was permitted during the task. What the Kovacs et al. (2009a, b) experiments have demonstrated is that when attention splitting features of a task are reduced in the testing environment, the effect of the Lissajous feedback is very powerful allowing participants to tune-in their motor capabilities and perform various difficult patterns of bimanual coordination with very low relative phase error and variability. An interesting feature however is that participants are apparently highly dependent on the information that the Lissajous feedback provides. Indeed, Kovacs et al. (2009a) found that levels of continuous relative phase error and variability where remarkably low when tested after 5 minutes of practice with concurrent Lissajous feedback available, suggesting that, the Lissajous plot and template provided participants a means by which they were able to detect their errors and perform the necessary corrections, in other words a short-term adaptation. On a

subsequent test however, when Lissajous feedback was removed, values of error and variability increased significantly indicating that participants were not able to perform the required coordination pattern. Participant's dependence on the concurrent feedback suggests that they had not developed an internal representation of the task, which they could rely on in the absence of concurrent feedback. This observation is consistent with the findings that suggest the existence of distinct cortico-cortical and subcortico-cortical neural pathways for externally (augmented feedback) and internally guided cyclical bimanual movements (e.g., Debaere et al., 2001, 2003) providing a neurophysiological account for the beneficial effect of providing augmented visual feedback to optimize movements.

Concurrent and terminal feedback information regarding the outcome of the movement has been perceived as one of the most important variables in the learning of motor skills (Adams, 1971; Bilodeau & Bilodeau, 1958). The guidance hypothesis postulates that although frequent feedback presentation provided during practice guides the learner toward the correct response, it also leads toward a dependency on that source of extrinsic feedback and blocks the processing of other important sources of information (Bjork, 1988; Schmidt, 1991) that are necessary to produce the movement when feedback is withdrawn on retention and transfer tests (Salmoni et al., 1984). For example, Winstein & Schmidt (1990) found no differences in performance between a 100% and 50% relative KR frequency group during acquisition. However, on a 5 minutes and 24 hours delayed retention test with no KR, a clear learning effect was shown that favored the 50% group, suggesting that reduced relative frequency feedback

was beneficial to learning. Additional experiments have also demonstrated the beneficial influence of reduced frequency KR (e.g., Lee, White, & Carnahan, 1990; Sparrow & Summers, 1992; Weeks, Zelaznik, & Beyak, 1993).

In sum, there is compelling experimental evidence indicating that concurrent Lissajous plot is a very effective way of providing feedback during bimanual coordination tasks (e.g., Swinnen, Lee et al., 1997), however extensive practice is still required for participants to be able to perform the task with relatively low error and variability when metronomes are used to pace the movement and vision of the limbs is permitted. Additionally, Kovacs et al. (2009a, b) have demonstrated that by eliminating the metronome and covering the limbs performance levels after only 5 minutes of practice are comparable with those previously obtained after several days of practice. However, participants dependence on the extrinsic information provided by the Lissajous plot was demonstrated when this information was withdrawn (Kovacs et al., 2009a).

Therefore, the main purpose of this experiment was to determine if reduced frequency of Lissajous feedback will facilitate the internalization of a representation that will allow participants to effectively perform the bimanual coordination task in the absence of extrinsic feedback. It is hypothesized that presenting 50% KR in a fading schedule will improve performance on a subsequent test when visual feedback is removed. The method of presenting feedback in a fading schedule involves providing feedback relatively often during the initial stages of practice and then gradually withholding the presentation of feedback more and more toward the end of practice

(Winstein & Schmidt, 1990; Wulf & Schmidt, 1989). A secondary purpose of the present experiment was to determine if by simply increasing the amount of practice when providing 100% feedback will also facilitate the internalization of a representation of the required coordination pattern.

Method

Participants

College students (N=63) received academic credit for participation in the experiment. The participants had no prior experience with the experimental task and were informed of the specific purpose of the study. Participants were right-hand dominant as determined by self report. Informed consent approved by the IRB for the ethical treatment of experimental participants at Texas A&M University was obtained prior to participation in the experiment.

Apparatus

The apparatus used was the same as described in Experiment 1.

Procedure

Participants were randomly assigned to a 100% feedback (KR), 50% feedback or 0% Lissajous feedback conditions and to a 5, 10 or 20 minutes practice group prior to entering the testing room. All participants were informed that they had to attempt to continuously flex and extend their left and right limbs about the elbow in order to produce the desired relative phase relationship. The on-line data was used to project a cursor (small circle) on a screen directly to the front of the participant with the position of the left lever moving the cursor up (extension) and down (flexion). The movement of

the right lever resulted in moving the cursor left (flexion) and right (extension). Also projected onto the screen was a circle that represents a 1:1 pattern of continuous sinusoidal motion with a 90^{o} relative phase between two signals. The current position of the limbs was indicated by the cursor overlaid on the template with the participant's goal defined as moving the cursor in a way to match the general shape of the Lissajous template projected on the screen in front of them. The 100% feedback group was provided KR throughout every practice trial while the 0% feedback group received no KR whatsoever. For the 50% feedback group KR was presented in a fading schedule. Trials were of 30 seconds duration. For a block of ten trials feedback presentation under the fading schedule was presented as follows: 25-25-20-20-15-15-10-10-5-5 seconds for each consecutive trial. Participants in the 5 minutes condition practiced one block of 10 trials, while participants in the 10 and 20 minutes condition practice two and four blocks of ten trials respectively. After each trial, in which the cycling frequency of the limbs was less than 1Hz, the experimenter encouraged the participants to increase their movement speed without disrupting the intended movement pattern. Stability of the newly learned coordination pattern was assessed on a delayed (24 h) retention test with (KR test) and without the augmented feedback (no KR test), counterbalanced between participants.

Measures and data reduction

All data reduction was performed using MATLAB. The potentiometer signals representing the limbs' displacements were low-pass filtered with a second order dual pass Butterworth with a cutoff frequency of 10 Hz.

Bimanual measures

To examine the spatial-temporal coordination of the limbs' motion, the continuous relative phase (ϕ) between the two limbs was computed. Prior to computation of the continuous relative phase, displacement and velocity data for each limb was normalized in two steps. First the mean of each data series was subtracted from each data point in the series to mean center the time series around zero. Second, amplitude rescaling was done by dividing the positive and negative amplitudes with the maximum positive or negative amplitude value. The phase angle (θ_i) for each limb ($i = r, l$) was computed for each sample of the displacement time series using the following formula adapted from Kelso et al. (1986):

$$\theta_i = tan^{-1}[(dX_i/dt)/X_i]$$

with X_i representing normalized limb position and dX_i/dt normalized instantaneous velocity. Next, the continuous relative phase was computed by subtracting the phase angle of the left limb (θ_l) from the phase angle of the right limb (θ_r), $\phi = \theta_r - \theta_l$. Root mean square error (RMSE) of the continuous relative phase was used as a measure of the degree to which the goal relative phase ($\phi = 90°$) was achieved. The standard deviation (VE) of relative phase was used as a measure of stability of the performed coordination pattern.

Unimanual measures

Using the time series of displacement that was mean centered around zero, cycle duration was computed on a cycle basis with each cycle representing every other zero crossing (Z_C) in the displacement trace (Cycle duration = $Z_{Ci+2} - Z_{Ci}$).

Results

Root mean square error (RMSE), and variability (VE) of the performed relative phase were analyzed in a 3 KR condition (100%, 50% and no KR) x 3 Practice time (5, 10 and 20 minutes) x 2 Test (Lissajous and no-Lissajous) ANOVAs with repeated measures on Test. These results are presented in the bimanual performance section. Mean cycle duration was analyzed in a 3 KR condition (100%, 50% and no KR) x 3 Practice time (5, 10 and 20 minutes) x 2 Test (Lissajous and no-Lissajous) x 2 Limb (left and right) ANOVAs with repeated measures on Test and Limb. These measures are presented in the unimanual performance section. Duncan's new multiple range test and simple main effect post-hoc tests were performed when appropriate ($\alpha = 0.05$).

The main question of interest in the present experiment was whether a reduced feedback frequency can facilitate the development of an internal representation of the coordination task, that will enable participants to have similar levels of performance when Lissajous feedback is presented and when this feedback is withdrawn. Based on previous experiments (e.g., Kovacs et al., 2009a, b) it was anticipated that participants receiving feedback 100% of the practice time will perform the Lissajous test significantly better than the no-Lissajous test. Additionally, no differences in performance on the two tests were expected for participants who did not receive Lissajous feedback during practice. However, high levels of variability were expected during both tests for participants who did not receive extrinsic feedback, and also for participants receiving 100% feedback during the no-Lissajous test. These high levels of variability in turn might mask any improvement in performance related to practice effect

(and interaction for that matter) that was expected to occur for the group receiving feedback 50% of their practice time. Therefore an *apriori* comparison at various stages of practice (*t*-test) was planned on the performance error measures (RMSE) between participant receiving 50% feedback on the no-Lissajous test and participants receiving 100% feedback on the Lissajous test. The comparison was made between performance on the no-Lissajous test for participants receiving 50% feedback and performance on the Lissajous tests for participants receiving 100% feedback.

Bimanual performance

The analysis of RMSE of relative phase detected a main effect of Test, $F_{(1,54)} = 20.43$, $p < 0.01$, with Duncan's new multiple range test indicating that participants had lower RMSE values during the Lissajous test compared with the no-Lissajous test (Figure 6A and 6B). The KR condition x Test interaction was also significant, $F_{(2,54)} = 10.01$, $p < 0.01$. Simple main effect analysis indicated that participants in the 100% KR and the 50% KR conditions made fewer errors when Lissajous feedback was available during testing compared to when Lissajous feedback was not available (Figure 6C). No such differences were detected for participants in the 0% KR condition, which performed the tests similarly under both feedback conditions. Additionally, participants in the 0% KR group made more errors during the Lissajous test compared to participants in the 100% and 50% KR groups which were not different from each other. During the no-Lissajous test, participants in the 100% feedback group performed the task with more errors than participants in the 50% and 0% feedback group which were not different from each other. All other main effects and interactions failed to reach significance.

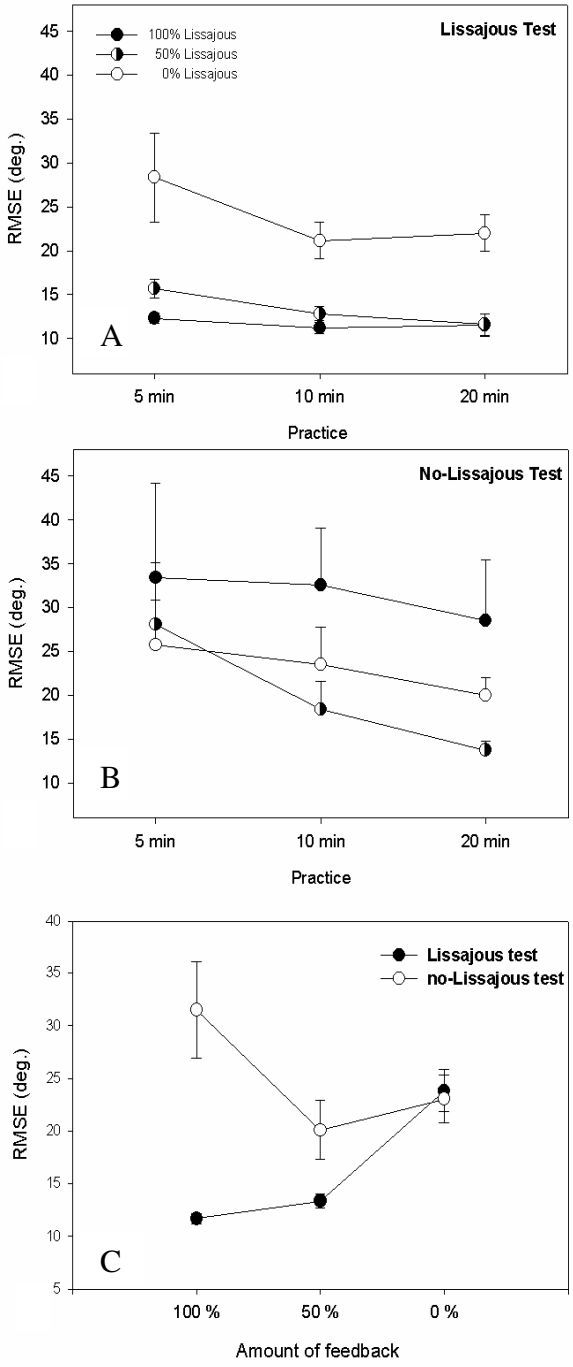

Figure 6. Relative phase error. RMSE for participants during the Lissajous (A) and no-Lissajous tests (B) as a function of practice time, and as a function of feedback condition (C). Error bars represent standard error of the mean.

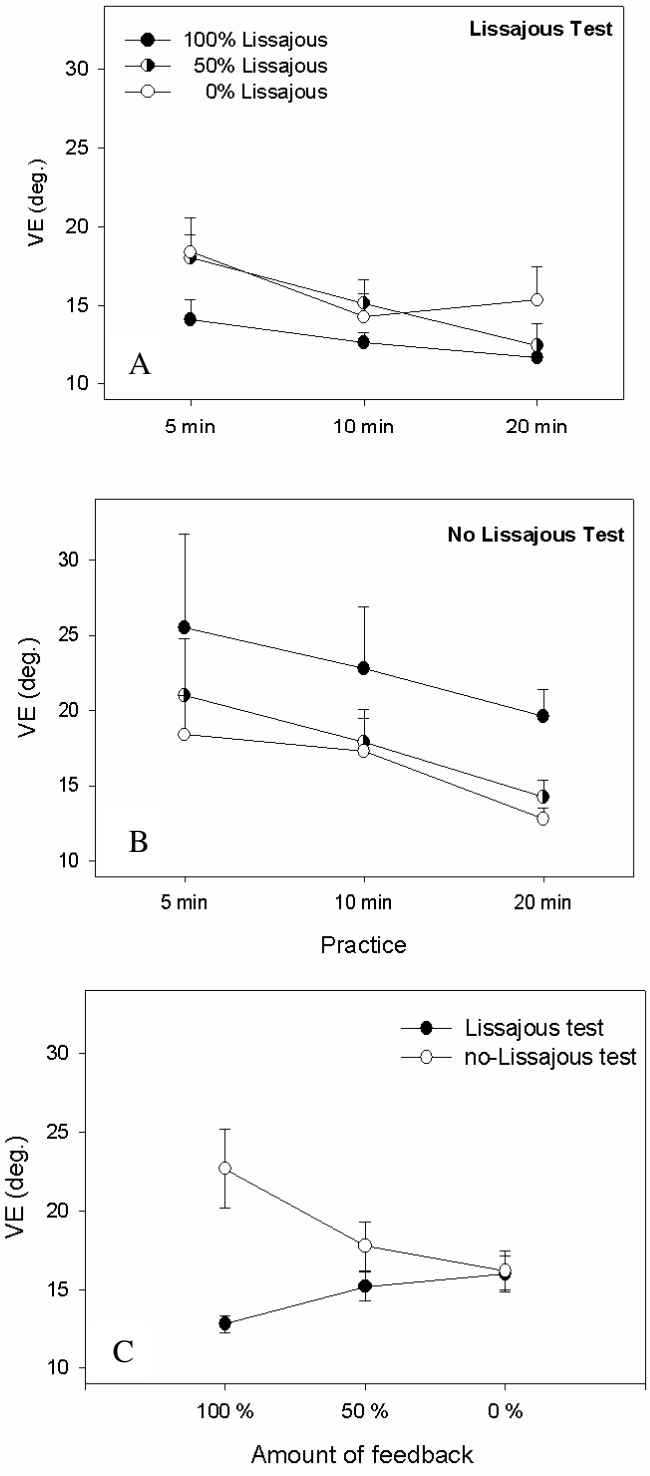

Figure 7. Relative phase variability. VE for participants during the Lissajous (A) and no-Lissajous tests (B) as a function of practice time, and as a function of feedback condition (C). Error bars represent standard error of the mean.

In terms of variability of performance (VE), the analysis detected a main effect of Practice time, $F_{(2,54)} = 5.02$, $p < 0.05$, with Duncan's new multiple range test indicating that performance in general was less variable after 20 minutes of practice compared with 5 minutes of practice. Also variability of performance after 10 minutes of practice was not significantly different compared with the 20 minutes and 5 minutes practice conditions. Main effect of Test was also significant, $F_{(1,54)} = 14.67$, $p < 0.01$, participants being more variable in their performance when Lissajous feedback was not available during testing compared to when Lissajous feedback was available (Figure 7A and 7B). Additionally, the analysis detected a significant KR condition x Test interaction, $F_{(2,54)} = 7.00$, $p < 0.01$. Simple main effect analysis indicated that participants who received 100% KR were more variable during the no-Lissajous test compared with the Lissajous test. Similarly, participants who received 100% KR were more variable during the no-Lissajous test compared with participants who received 50% KR and 0% KR, which in turn were not different from each other (Figure 7C). Although as expected, the analysis did not detect a practice effect suggesting that in general no improvement was made with additional practice, participants who received 50% feedback did improve their performance. This is best illustrated by the *apriori* comparisons at various stages of practice between participants receiving 50% feedback (no-Lissajous test) and participants receiving 100% feedback (Lissajous test). The analysis indicated that after 5 minutes of practice participants who received feedback 50% of the time in a fading schedule had considerably higher RMSE values compared with participants who received feedback 100% of the time $t_{(12)} = 4.63$, $p < 0.05$. After 10 minutes of practice,

although the performance of the 50% feedback group has improved, the difference compared to the group receiving 100% feedback was still significant, $t_{(12)} = 3.26$, $p < 0.05$. After 20 minutes of practice however, the analysis failed to detect a difference between the two groups, $t_{(12)} = 1.33$, $p > 0.05$. In other words, after 20 minutes of practice participants who received feedback 50% of the time they practiced, performed a test where no Lissajous feedback was available equally well as participants who had received 100% feedback have performed a test where Lissajous feedback was provided (Figure 8).

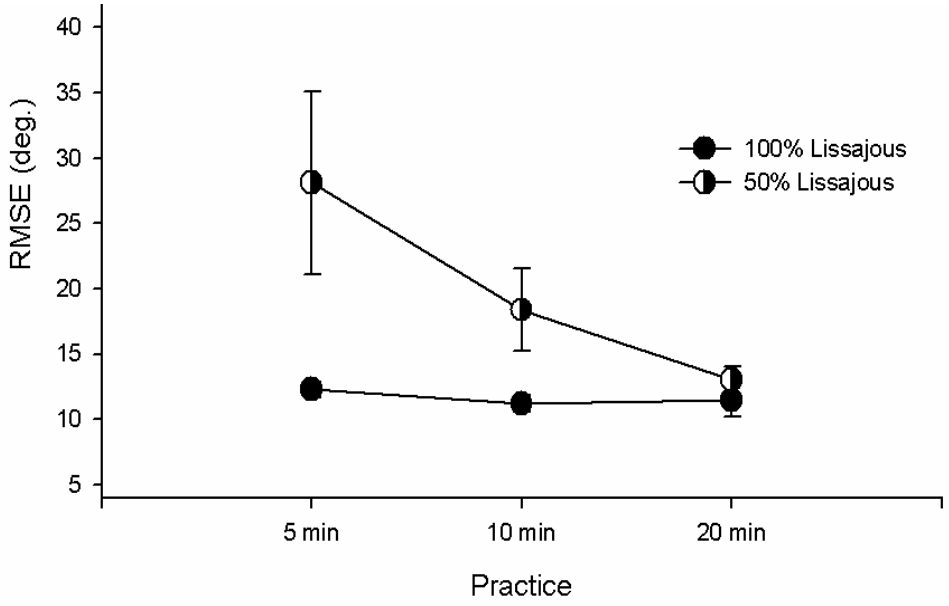

Figure 8. Relative phase RMS error. RMSE values at various stages of practice for participants receiving 50% feedback (no-Lissajous test) and participants receiving 100% feedback (Lissajous test). Error bars represent standard error of the mean.

Unimanual performance

The analysis of the mean cycle duration data failed to detect a difference between the groups that received different amounts of feedback, $F_{(2,54)} = 0.73$, $p > 0.05$ as well as between the groups that practiced for a different amount of time, $F_{(2,54)} = 0.84$, $p > 0.05$. Similarly, no differences between the left and right limbs were detected, $F_{(1,54)} = 0.26$, $p > 0.05$, and, mean cycle duration was also similar during the Lissajous and no-Lissajous tests, $F_{(2,54)} = 1.94$, $p > 0.05$. All interactions failed to reach significance, therefore the discussion will resume addressing the findings of the bimanual measures.

Discussion

The present experiment was designed to examine whether reduced feedback frequency presented in a fading schedule facilitated the internalization of a 1:1 bimanual coordination pattern with a 90^{o} relative phase offset. The purpose was to determine if participants were able to perform the required coordination pattern when the extrinsic Lissajous feedback was removed, after having received a reduced amount of feedback during practice. Note that previous research using Lissajous plots found remarkably low levels of relative phase error and variability while performing various difficult bimanual coordination patterns after only a few minutes of practice (Kovacs et al. 2009a, b), but also demonstrated participants dependence on the feedback as illustrated by dramatically increased levels of error and variability when the extrinsic information was removed. Thus, the main purpose was to determine whether the powerful effect of the Lissajous feedback can be combined with a feedback presentation schedule that will facilitate learning of a bimanual coordination task.

Participants coordinated rhythmic movements of their forearms while being provided concurrent Lissajous feedback with either 100% frequency, 50% frequency in a fading schedule or 0% frequency (no feedback). The task was to maintain a 90^0 phase relationship between limbs, and the amount of practice was 5, 10 or 20 minutes. By comparing relative phase error and variability on delayed retention and transfer tests, with and without Lissajous feedback, after various amounts of practice, it was possible to determine the extent to which participants were able to develop an internal representation of the required bimanual coordination task.

As previous research has shown (Kovacs et al., 2009a, b), after only 5 minutes of practice participants receiving 100% feedback were very effective (low error and variability) in producing the required coordination pattern when Lissajous feedback was provided. However, when the feedback was withdrawn, error and variability of relative phase increased, indicating considerable decrease in performance. The same pattern of results was observed after 10 minutes and 20 minutes of practice. Additionally, regardless of the amount of practice, participants receiving 100% feedback did not improve their performance on the delayed test with Lissajous feedback available. Similarly, when Lissajous feedback was not available during testing, performance did not improve with additional practice. In other words, more practice while receiving 100% feedback did not help participants to develop an internal representation of the task. This result in itself is quite surprising, considering the ubiquitous findings that in general more practice benefits learning. That is, all things being equal, more learning will occur if there are more practice trials. It is possible, however, that the availability of the

Lissajous feedback prompted participants to primarily rely on this source of information to guide their movements (Blandin, Toussaint, & Shea, 2008), which might also have prevented them to process information necessary for learning the task in a relatively permanent way (e.g. Schmidt & Bjork, 1992). Indeed, the guidance hypothesis postulates that on no KR trials in reduced frequency of feedback conditions (i.e. 50%) participants must rely and/or explore other sources of information during the practice phase. This additional processing results in participants learning something additional/different, such as the capability to detect one's own errors or to be consistent. In other words, too much feedback during practice is detrimental if the goal is to be able to produce the movement without the availability of feedback on a delayed test.

Indeed, participants who received reduced frequency feedback (50%) improved considerably their performance on a delayed test, when Lissajous feedback was withdrawn. In fact, after 20 minutes of practice, relative phase error and variability on the no-Lissajous test were comparable to the values of the group receiving 100% relative frequency feedback during the Lissajous test. The effect of reduced frequency feedback advantages in learning a novel motor task is not particularly remarkable in itself, many studies having reported similar findings (e.g., Armstrong, 1970; Lee et al., 1990; Sparrow & Summers, 1992; Weeks et al., 1993; Winstein & Schmidt, 1990). However, research typically testing the effects of various reduced frequency feedback schedules have assessed the degree of internalization of a novel motor task by using a delayed retention test where feedback was not provided (Schmidt & Wulf, 1997). Thus, participants who received 100% relative frequency feedback were facing a novel

situation during testing with no feedback available. In general the role of reduced frequency feedback is to facilitate the internalization of a novel motor task to the point where levels of performance when tested without feedback are comparable to performance levels obtained when feedback is available during testing. Using this logic, results from previous research are not as straightforward in illustrating the advantages of reduced frequency feedback. Although such a direct comparison has not usually been made it appears that, given a similar amount of practice, performance of a group receiving 100% feedback frequency is considerably better compared with the performance of a group that received reduced relative frequency feedback. Therefore, the results of the present experiment showing that participants are capable of performing a difficult coordination pattern when feedback is withdrawn as well as when feedback is available, is quite remarkable.

Finally, performance of participants receiving 0% feedback during practice was similar on both tests (with and without Lissajous feedback). Continuous relative phase error was relatively high, indicating that participants were not performing the required phase relation. This finding is consistent with the notion that performing a coordination pattern with 90^{o} relative phase is quite difficult for a system whose intrinsic dynamics exhibit stability at 0^{o} and 180^{o} relative phase (Kelso et al., 1986) but not at other phase relations. Additionally, in the absence of extrinsic feedback, it is quite obvious that participants were not able to significantly improve their performance with the limited amount of practice provided in the present experiment. However, even with limited practice participants were able to reduced their variability, especially when tested

without the Lissajous feedback. In sum, when Lissajous feedback was not provided during practice, performance did not improve, but movement variability decreased as a function of practice indicating that participant's performance became more stable.

When attentional demands are decreased through the absence of metronomes to pace the movements (Kovacs et al., 2009a), the limbs are covered to avoid distractions (Kovacs et al., 2009c), and Lissajous feedback (goal pattern and cursor representing the position of the limbs) is presented, participants are capable of tuning-in their motor responses to produce difficult patterns of bimanual coordination with low levels of continuous relative phase error and variability, comparable to levels typically attained after several days of practice (Swinnen, Lee et al., 1997). However, when the salient Lissajous feedback was removed, performance levels considerably deteriorated (Kovacs et al., 2009a). What the present experiment demonstrates is that salient extrinsic feedback (in the form of Lissajous plot and template) can be effectively combined with reduced frequency feedback presentation in a way that performance levels, when tested without the availability of feedback, match those obtained when tested in the presence of Lissajous feedback.

CHAPTER V

CONCLUSION AND RECOMMENDATIONS

Two experiments were proposed, aimed at providing further understanding of how previously identified intrinsic constraints and perceptual factors interact in influencing the performance of various bimanual coordination patterns. Experiment 1 was intended to determine if the strong coupling asymmetries manifested between dominant/non-dominant limbs and between limbs moving with disparate amplitudes can be overcome when salient integrated perceptual feedback is provided and attentional demands are reduced. It was hypothesized that asymmetric coupling between the limbs arises in part from perceptual-attentional demands present in the testing environment. Experiment 2 was aimed at determining the degree of reliance on the salient and integrated visual feedback, more specifically to determine whether the powerful effect of the Lissajous feedback can be combined with a feedback presentation schedule that will facilitate learning of a bimanual coordination task. It was hypothesized that presenting 50% reduced frequency feedback in a fading schedule will improve performance on a subsequent test when visual feedback will be removed.

The findings from the present experiments are consistent with recent bimanual coordination research (Kovacs et al., 2009a-c, in press; Mechsner et al., 2001), visuo-motor tracking research (Wilson et al., 2005a, b; Ryu & Buchanan, 2009), and even rapid aiming research constrained by Fitts' Law (Kovacs, Buchanan, & Shea, 2008) which report that salient perceptual information can override some aspects of the system's intrinsic dynamics typically linked to motor output control. The strong

tendencies toward the intrinsic dynamics found in numerous previous bimanual movement studies and the difficulties in producing various coordination patterns may actually represent detrimental effects attributable to the perceptual information available in the environment and the attentional focus participants adopt. Given external integrated salient visual information participants can essentially tune-in difficult bimanual coordination patterns with little practice.

Note that much of the difficulty in performing various coordination patterns has been attributed to intrinsic neuromuscular constraints that tend to pull the system toward more stable intrinsic coordination patterns. Moreover, when performing coordination patterns with disparate amplitudes, the intrinsic neuromuscular constraints are thought to be "enhanced" due to increased neural activity required by an increase in movement amplitude. However, given salient visual information, participants can very effectively perform (low error and variability of relative phase) coordination patterns when the limbs are required to move at different amplitudes. These findings suggest that the notion of neural crosstalk (forward command streams as well as the integration of proprioceptive feedback) must be viewed as a highly dynamic concept, susceptible to perceptual interferences, and not as rigid "prewired" neuro-anatomical constraints. Moreover, this notion seems to be supported also by the finding that participants are capable of rapidly developing an internal representation of a relatively difficult coordination pattern ($\Phi = 90^{o}$) that allows them to perform the task quite effectively in the absence of the Lissajous feedback.

The notions of increased difficulty and increased variability of various coordination patterns have been consistent with much of the previous research on bimanual coordination. Data from the present experiments however, and that of other recent experiments using a similar protocol (Kovacs et al., 2009b-c, in press) provide a quite different picture (see Figure 9). When attentional demands are reduced, and Lissajous feedback is presented errors and variability in continuous relative phase remain remarkably low and relatively constant across a wide variety of coordination requirements with only the 1:1 in-phase coordination pattern resulting in lower errors and variability. In Figure 9 continuous relative phase errors and variability are plotted for the bimanual tasks used in the present experiments (B) and bimanual task used in recent experiments (Kovacs et al., 2009b-c, in press) using similar protocols (A). What this comparison yields is the finding that 1:1 in-phase results in approximately 5^{o}-6^{o} continuous relative phase error and variability, while all other bimanual conditions tested with Lissajous feedback resulted in roughly 10^{o}-12^{o} errors and variability. Note that proprioceptive feedback and neural crosstalk arising from forward command streams are thought to be complementary for 1:1 in-phase ($\Phi = 0^{o}$), but not for other phase relationships. However, in the present experiments and other recent experiments using similar protocol (Kovacs et al., 2009b-c, in press), these potential constraining factors (proprioception and neural crosstalk) that might be contributing to error and variability of performance, were not controlled. Therefore, by minimizing attentional factors and increasing the saliency of the perceptual factors during bimanual coordination, dramatically decreases levels of relative phase error and variability across a wide variety

of coordination patterns, it appears that there is a relatively constant source that contributes to increasing these levels of variability and error in all the coordination patterns relative to the 1:1 in-phase pattern.

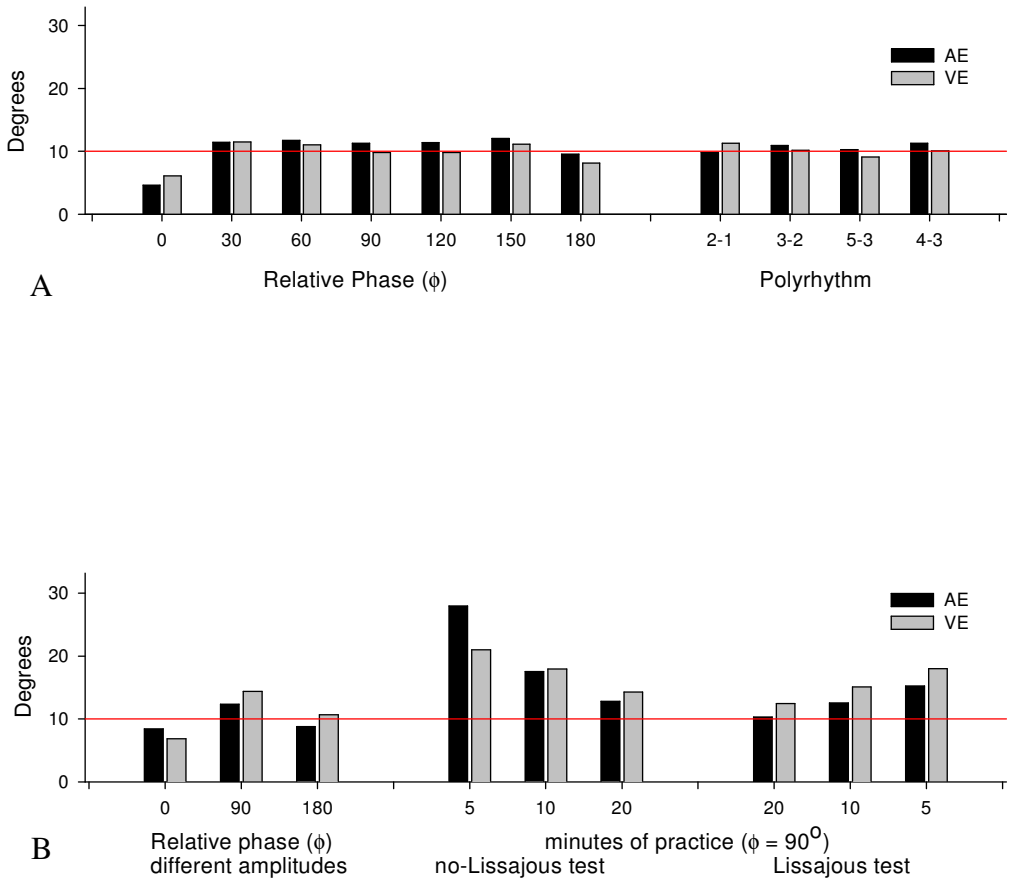

Figure 9. Cross experiment comparison of error and variability. Absolute error (AE) and variability (VE) in continuous relative phase from the present experiments (B) are compared with recent experiments using similar protocols testing phase lags of 0^{o} – 180^{0} in 30^{o} increments (Kovacs et al. 2009b) and multi-frequency 2:1 and 3:2 (Kovacs et al. 2009c) bimanual coordination patterns, and 5:3 and 4:3 (Kovacs et al. in press) bimanual coordination patterns.

The experimental protocols used in the present and more recent experiments (Kovacs et al., 2009a-c, in press) can potentially provide for future research a basis to evaluate the magnitude of additional constraints (i.e., proprioception and neural crosstalk) by essentially minimizing the error and variability due to attentional and perceptual factors.

The development of equations of motions in the form of non-linear coupled oscillator models and potential function models to capture the formation of stable coordination patterns and transitions between stable coordination patterns has been a primary feature of the dynamic pattern approach (Kelso, 1995; Kelso et al. 1986; Haken et al. 1985). The phase transitions from anti-phase to in-phase coordination, as well as the accompanying stability-related phenomena, have been modeled by Haken et al. (1985), arguing that the simplest potential function (HKB model) that can account for the observed transition in coordination is

$$V(\Phi) = - a \cos\Phi - b \cos(2\Phi),$$

with Φ denoting relative phase (Figure 10).

Although the original formulation of the HKB model assumed identical oscillators and symmetrical coupling functions, Haken et al. (1985) already acknowledged the possibility of functional asymmetries in these respects. Indeed, a number of studies have shown that the coordination dynamics is influenced by particular characteristics of the moving limbs, handedness and focus of attention to one or the other limb. For example, difference in eigenfrequencies of the limbs results in changes in pattern stability and phase drift (e.g., Jeka & Kelso, 1995).

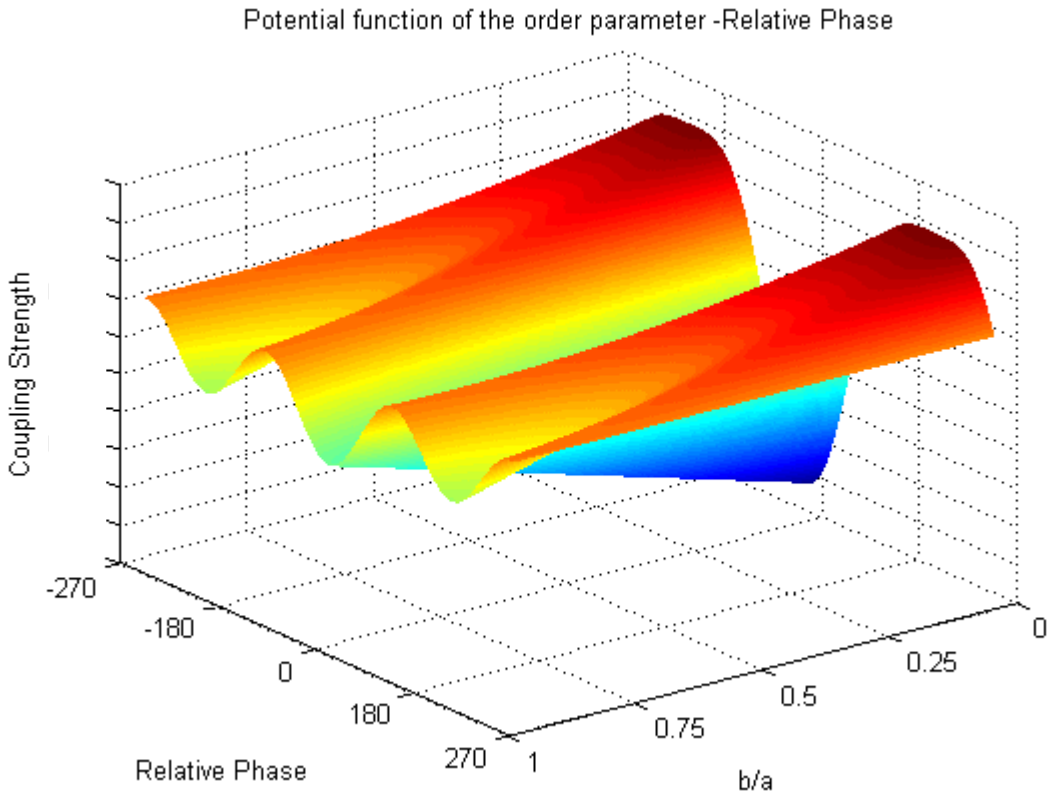

Figure 10. The HKB model of coordination. The potential, V(Φ), as the ratio b/a changes.

To capture the influence of different eigenfrequencies an additional component, referred to as the detuning parameter ($\Delta\omega$), was introduced into the order parameter equation (Kelso, DelColle, & Schöner, 1990):

$$d\Phi/dt = \Delta\omega - a \sin\Phi - 2b \sin(2\Phi)$$

Note that the order parameter equation was derived to express the dynamics of the order parameter (relative phase) given the relation:

$$d\Phi/dt = - dV(\Phi)/d\Phi,$$

thus

$$d\Phi/dt = - a \sin\Phi - 2b \sin(2\Phi).$$

More importantely, a difference in eigenfrequency (preferred movement frequency) has been shown to be mediated by disparate movement amplitudes of the two component oscillators (Beek et al., 1996). Other studies have observed asymmetries in the performed relative phase as an effect of handedness (e.g., Treffner & Turvey, 1995; de Poel et al., 2007) with the right limb on average leading the left limb in time for right-handers, and the left limb leading the right for left-handers. Similarly, when attention was directed toward the dominant limb, the phase lead of the dominant limb was found to be larger than when the non-dominant limb was attended (e.g., Amazeen et al., 1997). To account for these effects, the original symmetry of the HKB model was broken by incorporating additional terms into the order parameter equation. For example, to accommodate the handedness related asymmetries, Treffner & Turvey (1995) incorporated two additional cosine terms to the order parameter equation:

$$d\Phi/dt = - a \sin\Phi - 2b \sin(2\Phi) - c \cos\Phi - 2d \cos(2\Phi).$$

In the extended model, the parameter d was proposed to capture the influence of handedness (Treffner & Turvey, 1995), as well as the influence of asymmetric attention (Amazeen et al., 1997) on the relative phase dynamics.

Combining the additional terms introduced into the order parameter equation leads to

$$d\Phi/dt = \Delta\omega - a \sin\Phi - 2b \sin(2\Phi) - c \cos\Phi - 2d \cos(2\Phi).$$

More recently, Bingham (2004a) has argued that the origin of the potential function in the HKB model resides in the informational coupling between the limbs, and therefore

proposed a perceptually driven nonlinear dynamical model. At the basis of the perceptually driven model was the hypothesis that relative phase (Φ) and relative phase variability are perceptible properties, with the perceived phase variability being dependent on the velocity differences between oscillators. Similarly, Wilson & Bingham (2008) found that relative direction is the information used to perceive relative phase during in-phase and anti-phase coordination, and in order to be able to perceive a coordination pattern with 90^{o} relative phase, a new variable composed of position and speed needs to be learned. The work of Bingham and colleagues (Bingham et al., 1999; Bingham, 2004a, b; Wilson et al., 2005a, b; Wilson & Bingham, 2008) has provided a major contribution to linking perception and action in bimanual coordination tasks. Nevertheless the perceptually driven model of coupled oscillators produces patterns of stability and attraction similar to the HKB model.

The primary purposes of extending the basic HKB model were to accommodate functional asymmetries and/or constraints that have been experimentally shown to influence the coordination dynamics. What the present experiments and other recent experiments using similar protocols (Kovacs et al., 2009a, b) demonstrate, is that some of the functional constraints found in previous research might actually be attributable to attentional and perceptual factors present in the testing environment. These findings suggest that when attentional demands are reduced and salient visual feedback is provided, participants can override some aspects of the system's intrinsic dynamics typically linked to motor output control. Thus, future models of bimanual coordination must take into account how perceptual factors can free the action component of the

perception-action system from previously identified constraints. Indeed, a variety of coupled oscillator systems, involving different coupling functions, may result in the potential function identified by the HKB and other extended models. What future research needs to determine is whether the results of the present experiments and other recent experiments using similar protocols (Kovacs et al., 2009a, b) can be accommodated by further extensions of the HKB model, or new models need to be developed.

Complementing recent research showing that provided the above testing conditions participants can perform various difficult coordination patterns with low levels of error and variability, the present research shows that participants can also develop an internal representation of the required coordination pattern and perform the task without receiving concurrent feedback at similar levels of performance as when feedback is provided. Therefore, future models of bimanual coordination must take into account whether or not the task is primarily requiring a long-term modification in motor output, or just a tuning of motor capabilities within a given context.

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Research Publications

1. **Kovacs, A.J.**, Boyle, J., Gruetzmacher, N., & Shea, C.H. (*in press*). Coding of on-line and pre-planned movement sequences. *Acta Psychologica,*

2. **Kovacs, A.J**., Buchanan, J.J., & Shea, C.H. (*in press*). Impossible is nothing: 5:3 and 4:3 multi-frequency bimanual coordination. *Experimental Brain Research*,

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